RESISTANCE OF SELECTED GRASSES TO FALL ARMYWORM, *Spodoptera frugiperda* (J. E. SMITH)

BY

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To my parents

and

parents-in-law

Without their help and encouragement,

this work could scarcely have been done.

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RESISTANCE OF SELECTED GRASSES TO FALL ARMYWORM, *Spodoptera frugiperda* (J. E. SMITH)

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The interactions and relationships of fall armyworm, *Spodoptera frugiperda* (J. E. Smith), and selected grasses were studied in this research. Larvae showed a significant orientation to the chemical stimuli from all the grasses but showed no chemotactile preference in paired comparisons for the grasses. Multiple choice preference tests indicated that Tifton 10 bermudagrass [*Cynodon dactylon* (L.) Pers] was most preferred, followed by Coastal bermudagrass, common centipedegrass [*Eremochola ophiuroides* (Munro) Hack.], C-181 centipedegrass, and Tifton 292 bermudagrass. Zoysiagrass (*Zoysia* sp.) was the most nonpreferred grass by fall armyworm larvae. Damage ratings confirmed the preference of larvae for Tifton 10 as it sustained 50 times more damage than zoysiagrass.

The preference of neonate larvae for centipedegrass was increased 9-fold, and the damage was increased 16-fold by applying nitrogen fertilizer once every two weeks.

Similarly, preference for and damage to Coastal bermudagrass was increased 15 times and 46 times, respectively, on fertilized vs. nonfertilized plants.

The nonpreference was found as one of the major resistance mechanisms of centipedegrass while Tifton 292 bermudagrass and zoysiagrass were unsuitable for fall armyworm feeding due to a high degree of nonpreference. Abnormal pupae with wing-area deformities and/or serious adult wing lesions were observed when these resistant grasses were incorporated into the pinto bean diet and fed to the larvae.

Development of larvae which previously fed on the preferred grasses was primarily dependent on the suitability of the grass to which the larvae were transferred. The suppression of larval growth was caused by low consumption rate and/or greater metabolic expenditures when larvae were switched from susceptible diets to resistant grasses. No compensation for low efficiency of food conversion by increasing relative consumption rate was found when larvae were transferred to the resistant grasses.

Both the effects of various host plants on the fall armyworm larvae and interactions of initial feeding time with host plants are suggested as relevant to the development and practical management of this pest.

CHAPTER I
INTRODUCTION

The fall armyworm (FAW), Spodoptera frugiperda (J. E. Smith), is one of the most persistent and destructive pests in the southeastern and central United States where it often attacks many economically important cereals and grasses (Crumb 1927, Luginbill 1928). The characteristics of high mobility and polyphagy of the FAW make it difficult to manage (Barfield 1979). Thus, the average annual crop losses caused by this pest exceed $300 million in this country (Mitchell 1979a).

Other than the important food and fiber crops (Hinds and Dew 1915, Luginbill 1928), the FAW is capable of severely damaging grasses which are grown as turf or pasture (Dew 1913, Kelsheimer et al. 1953, Koehler et al. 1977). Florida has over 3 million acres of improved pasture of which ca. 200,000 acres are grown for hay. Grasses used for silage, soil conservation, and roadside stabilization are also attacked by the FAW (Koehler et al. 1977).

Increased emphasis is being placed on the development of plant cultivars that resist or tolerate attack by the major insect pests of a particular crop (Painter 1958, Maxwell et al. 1972, Gallun et al. 1975). Screening the

resistant germplasm and defining the mechanisms of resistance as well as studying the environmental factors that condition resistance are all necessary components for the development and utilization of insect-resistant plant cultivars (Painter 1951).

Only recently have the studies with the FAW involved testing for resistance of different grasses (Wiseman and Davis 1979). However, the mechanisms of resistant varieties of grasses are not well understood. More basically, the biological or physiological performance of the FAW which feed on different grasses is also in question. The purpose of this research was to study the FAW-grass plant interactions and relationships.

CHAPTER II
LITERATURE REVIEW

Synonyms and Distribution

The fall armyworm was originally described in 1797 under the name Phalaena frugiperda Smith and Abbot. Subsequent treatments of this species assigned to it the following names: Laphygma macra Guen, 1852; L. inepta Walker, 1856; Prodenia signifera, 1856; P. plagiata Walker, 1856; P. autumnalis Riley, 1876; P. obscura Riley, 1876; Caradrina flavimaculata Druce, 1909 (Hampson 1909). Until recently, it was known for many years as Laphygma frugiperda Smith. However, Zimmerman (1958) indicated no important difference between the genera Laphygma and Spodoptera, and he suggested merging the genera. The currently accepted name is Spodoptera frugiperda (J. E. Smith), the fall armyworm (Todd 1964).

Luginbill (1928) described the FAW as having a tropical-subtropical origin in the Western Hemisphere. The distribution of this pest includes North America, Central America, South America, and the West Indies (Commonwealth Inst. Entomol. 1956). The FAW can infest almost the entire agricultural area of the United States in the summertime (Snow and Copeland 1969). However, in most winters, FAW

survival is limited to the extreme southern tips of Florida and Texas (Luginbill 1928, Tingle and Mitchell 1977), or along the Gulf Coast as suggested by Hinds and Dew (1915) and Vickery (1929).

Host Plants and Damage

Grasses and small cereal grains are usually the first choice as food of FAW larvae (Watson 1916, Crumb 1927), although it attacks other crops. Luginbill (1928) listed more than 60 species of plants attacked by FAW--most of them belong to the Graminae. The important economic crop plants are the following: corn (Zea mays L.), millet (Pancium spp.), oats (Avena sativa L.), rye (Secate cereale L.), rice (Oryza sativa L.), sorghum [Sorghum bicolor (L.) Moench], sugar cane (Saccharum officinarum L.), and wheat (Triticum aestirum L.). In addition to the Graminae plants, Hinds and Dew (1915) observed that more than 20 other crops including cotton (Gossypium spp.), soybean [Glycine max (L.) Bragg], peanuts (Arachis hypogaea L.) etc. are fed upon by this pest.

Types of damage caused by the larvae of the FAW, for most of crop plants, are defoliation, promotion of entry of plant pathogens, and death of the plant. Defoliation ranges from skeletonization of leaves by young larvae to complete consumption of entire leaves by old larvae (Luginbill 1928, Vickery 1929). The whorl, ear, and tassel can also be attacked when FAW larvae feed on corn (Burkhardt 1952).

The FAW was reported by Colonel Whitner as being particularly injurious on grass, corn, sugar cane, and upland rice in Florida as early as 1845 (Chittenden 1901). Mention was made also of a severe outbreak during the summer of 1912 by Walton and Luginbill (1916), when the FAW swept across almost the entire United States east of the Rocky Mountains.

Combining the records of FAW outbreaks since 1856, Sparks (1979) concluded that the outbreaks of the FAW have occurred in this country at very irregular intervals. From 1975 to 1977 heavy FAW infestations occurred throughout the southeast and along the Atlantic Coast (Sparks 1979). Especially in 1977, Florida pastures, hay fields and forage crops were attacked by large numbers of this pest (Koehler and Short 1979); in Georgia, losses in pasture and forage to the FAW in this year exceeded $59 million (Todd and Suber 1980). The average estimates of annual crop losses caused by this pest in United States exceed $300 million (Mitchell 1979a).

Artificial Diet and Mass Rearing

The comprehensive studies of FAW have been achieved by rearing this insect in the laboratory with a number of techniques. Artificial diets developed for rearing FAW were basically modified from the diets developed for rearing other insect species. George et al. (1960) developed an artificial medium for rearing the field-collected late

instar FAW. Revelo and Raun (1964) placed 1st-instar larvae on plant tissue; the 2nd-instar larvae were then transferred to vials containing the diet developed for the European corn borer, Ostrinia nubilalis (Hubner). Wiseman et al. (1970) tested the biology of FAW larvae with the agar-based diet containing corn kernels or leaves. The regular pinto bean diet of FAW (Burton 1967) was also modified by Wiseman et al. (1984) to determine the bioassay essential to detect differences between the susceptible and resistant grass palnt materials. In their study, larval weight differences were easily detected by feeding FAW on pinto bean diet without the Torula yeast adding the resistant or susceptible grasses.

The techniques, equipment, and cost of mass rearing FAW in the laboratory were reviewed by Perkins (1979). At the Insect Biology and Population Management Research Laboratory, Tifton, Georgia, FAW have been successfully reared for ca. 24 years (ca. 250 generations) since 1960. Three diets that have been successfully used at this laboratory are as follows: the casein wheat germ diet (Burton 1967), the pinto bean diet (Burton 1969), and the WSB diet (Burton and Perkins 1972).

+ Life History

General reviews of the FAW life cycle are illustrated by Walton and Luginbill (1916), Luginbill (1928), Vickery (1929), and Sparks (1979).

The adult FAW is about 1.8 cm in length, and 3.5 cm in wing-expanse. Adults initiate early evening movement near host plants. After a general feeding period, females initiate calling. Males travel at oblique angles to the wind and respond to the calling female from a distance of 30-40 feet. The mating activities peak prior to midnight, depending on temperature and time of season (Sparks 1979).

Oviposition by mated females occurs close to, and may overlap with, the early evening feeding period. Eggs are laid in clusters and are covered by a dense layer of scales. Thomson and All (1983) indicated that FAW egg masses are most prevalent on the under surface of corn leaves, and in the leaf region proximal (50% of leaf length closest) to the corn stalk. Egg masses contain from a few to hundreds of eggs, averaging about 200 eggs per cluster, which will hatch in 2-4 days if mean temperatures are 70-80° F (Sparks 1979, Combs and Valerio 1980b).

Some characteristics of FAW larvae include the following: prolegs on the third to sixth and tenth segments of the abdomen, mandibles with prominent teeth, five setae ventral of spiracle on the first abdominal segment, and conspicuous dorsal pinacula (Levy and Habeck 1976). The 1st-instar larvae are positively phototactic and cannibalistic. Their movements are greater at higher densities (Morrill 1971). On corn, FAW commonly feed on the leaves and in the ears (Walkden 1950). Also, they can bore into the corn stalks (Burkhardt 1952, Wiseman et al. 1967).

The sixth-instar larvae drop to the ground and pupate ca. 1-3 inches deep in the soil (Sparks 1979). No larvae survived to pupation at or below 14° C in a laboratory test (Morrill 1971). Uncommon pupation also occurs in ears, tassels and whorls of corn during outbreaks (Burkhardt 1952). Leuck and Perkins (1972) stated that there is a significant correlation between FAW pupal weight and adult fecundity of this insect.

The entire life cycle of FAW requires ca. 4 weeks in the southeastern United States in warm weather (Vickery 1929). When reared on bermudagrass, both larvae and pupae develop more rapidly at 30° C, and egg production is maximal at 25° C (Combs and Valerio 1980a).

The fall armyworm overwinters in a few southern coastal areas. Several articles have illustrated that southern Florida (Hastings and Homestead areas) may act as a reservoir for overwintering populations of FAW (Tingle and Mitchell 1977, Wood et al. 1979, Waddill et al. 1982). Every year this pest migrates from these refuges to infest crops as far north as Canada and as far west as Montana (Young 1979a).

Control and Management

Biological Control

Ashley (1979) summarized the published data on parasites reared from field-collected FAW. He indicated that 53 species (43 genera and 10 families) have been reported as

parasites of the FAW. The braconids, ichneumonids, and tachinids accounted for most of the parasites; Apanteles marginiventris (Cresson) and Chelonus texanus (Cresson) are the parasites recovered most frequently from FAW larval collections. Andrews (1980) mentioned 5 families, which included 9 genera and 11 species, of FAW parasites from Central America. Ashley et al. (1983) found that in southern Florida the major parasite of FAW on corn is Chelonus insularis Cresson, and A. marginiventris (Cresson) is the principal parasite of FAW on bermudagrass [Cynodon dactylon (L.) Pers]. Pair and Gross (1984) reported the first ichneumonid parasitoid, Diapetimorpha introita (Cresson), which attacks FAW in the pupal stage.

The fall armyworm is susceptible to at least 16 species of entomogenous pathogens including viruses, fungi, protozoa, nematodes, and bacteria (Gardner and Fuxa 1980). Field applications of these entomogenous pathogens effectively suppressed this pest, especially with the Spodoptera frugiperda nuclear polyhedrosis virus sprayed in corn fields (Hamm and Young 1971), the bacterium, Bacillus thuringiensis Berliner, in cabbage (Creighton et al. 1964, 1972), and the nematode, Neoaplectana carpocapsae in corn (Landazabal et al. 1973). Recently, Rohlfs and Mack (1984) indicated that when FAW density increased, the parasitization rate of Ophion flavidus Brulle increased in a nonlinear manner, and the parasitized FAW larvae consumed less food, gained less weight, and had higher approximate digestibility values compared to unparasitized larvae (Rohlfs and Mack 1983).

Pheromone Traps

Four related pheromone compounds have been identified from virgin females of FAW (Sparks 1980). The (Z)-9-dodecen-1-ol acetate and (Z)-0-tetradecen-1-ol acetate (Sekul and Sparks 1967, 1976) are the two major components of the FAW pheromone which can be used in monitoring and managing populations of the FAW (Mitchell 1979b). Tingle and Mitchell (1975) used pheromone bait as a lure to compare the effectiveness of traps in capturing males. They also conducted pheromone trap placement studies around corn, peanuts and grass in north Florida (Tingle and Mitchell 1979). Mitchell and McLaughlin (1982) found, by using the air permeation technique, that mating and oviposition of FAW were reduced by 86 and 84%, respectively, in a corn field after the application of (Z)-9-tetradecen-1-ol acetate. However, the potential use of pheromones for population management of FAW will be decided only when their effect on infield mating is determined over large acreages (Sparks 1980).

Chemical and Cultural Control

The insecticidal control of FAW is often necessary in producing crops. Generally, control of this pest is achieved by using a systemic insecticide applied at planting (Young 1979b). Environmental Protection Agency approved FAW control on corn, sorghum, and pasturage with carbaryl, trichlorfon, methyl and ethyl parathion, diazinon and methomyl.

Permethrin also provided significant mortality of FAW on pasturegrass (Koehler and Short 1979). Young (1980) reported that in corn, FAW control was achieved with 0.1 and 0.3 in (2700 and 8100 gal) water/acre when chlorpyrifos + oil was applied in irrigation water with a center-pivot irrigation system. Field studies demonstrated that the resistance to insecticides of the FAW include carbaryl and trichlorfon, but not methomyl (Bass 1978).

The effects of different host plants on the susceptibility of FAW to insecticides are quite variable. Combs and Chambers (1979) indicated that the strain of first-instar FAW collected on cotton or corn was more tolerant to insecticides than the laboratory strain. However, Roberts (1965) fed FAW of similar weights with different host plants and showed no difference in susceptibility to several insecticides. Recently, Wood et al. (1981) treated FAW larvae weighing ca. 20-30 mg with 4 different insecticides and found that larvae reared on bermudagrass and millet [Pennisetum americanum (L.) Lecks] were more susceptible to carbaryl and permethrin than larvae reared on corn, cotton, or soybean. The different microsomal oxidases (MFO) were shown to be induced in different levels by feeding FAW larvae on various host plants and thus, the susceptibility of this pest to various insecticides was influenced (Yu 1982a, 1982b, 1983a, Yu and Ing 1984).

The effects of fertilization, harvest frequency and insect control on yield of Coastal bermudagrass were

evaluated to develop management skills for the cultural manipulation of FAW by Lynch et al. (1980). They indicated that a split application of nitrogen, applied by 1 June, will produce greater than 80% of the annual yield by 1 August. Altieri (1980) also demonstrated that the diversification of the corn ecosystem could be used as a means of regulating FAW populations. Examples include the corn-bean polycultures in Colombia (Altieri et al. 1978) and the corn-weed associations in Florida (Altieri 1979).

The economic thresholds for the FAW on grain sorghum have been estimated as 1) 10% of seedling sorghum possessing egg masses, 2) 1 larva/plant in the whorl stage, and 3) 2 larvae/head after flowering. In Coastal bermudagrass, the action threshold is between 2-10 larvae 3/8 in. long/ft^2 (Martin et al. 1980). In further study, Alvarado et al. (1983) indicated that the economic injury level for FAW on Alicia bermudagrass was 0.67 third- to sixth-instar larvae per sweep in 2 to 15 cm grass sampled at 2:00 to 3:00 p.m.

Plant Resistance

Painter (1951) defined resistance as " . . . the relative amount of heritable qualities possessed by the plant which influence the ultimate degree of damage by the insect." Luginbill (1969) stated that the resistant plants are "the most effective and ideal method of combating insects that attack crop plants." The FAW, however, has

been studied less from the insect/plant relationship viewpoint until recently (Wiseman and Davis 1979).

Brett and Bastida (1963) indicated that resistance in some varieties of sweet corn is due to tolerance to FAW feeding, although Horovitz (1960) searched unsuccessfully for corn varieties in Venezuela resistant to the FAW. Wiseman et al. (1966) began the extensive and intensive search for seedling resistance to this pest by screening several thousand corn lines. They demonstrated differences in damage among corns in both the seedling and mature stages, where the "Antigua" corns were among the least damaged (Wiseman et al. 1967). The resistance in "Antigua" corn could be increased or decreased simply by the manipulation of fertilizer (Wiseman et al. 1973a, 1973b). Scott et al. (1977) were the first to release the resistance corn germplasm ("Mp 496") that has "Antigua Gp 2" in its background. Nevertheless, not until 4 years later was the resistance mechanism of "Antigua 2D-118" to FAW determined as nonpreference, and "MpSWCB-4" was both nonpreference and antibiosis (Wiseman et al. 1981). Widstrom et al. (1972) analyzed the feeding injury data for 8 corn inbreds and their F_1 to determine the gene action of the resistance of corn to FAW. The general combining ability was concluded highly significant, while dominance and/or specific combining ability were unimportant in conditioning corn resistance to FAW. Moreover, Williams et al. (1978) reported that the relative importance of general and specific

combining ability may depend on the severity of the infestation.

McMillian and Starks (1967) reported that FAW damage to sorghum differed significantly with variety. Anderson and Cherry (1983) tested 15 varieties of sorghum and found "Richardson Sugar Red" having the least amount of FAW feeding damage. Plant height and maturity were also shown in this study as significantly negatively correlated with FAW damage among varieties. Schwager et al. (1984) screened 25 sorghum lines in the field and found that none of these varieties demonstrated acceptably levels of resistance to FAW feeding. However, the high genetic variability in sorghum species makes it an attractive candidate for breeding programs to develop insect-resistant varieties (Wiseman and David 1979).

Leuck et al.(1967) compared 14 peanut lines and found that only one cultivar of peanuts, Southeastern Runner 56-15, possessed resistance to the FAW. This cultivar was further shown to debilitate the development of FAW by increasing the length of the life cycle and decreasing the percentage of moths that emerged (Leuck and Skinner 1971). Barfield et al. (1980b) emphasized the influence of peanut plant phenology on the FAW. In their study, FAW larvae consumed more leaf tissue on intermediate aged plants (67-92 days) than on younger (45-70 days) or more mature (92-120 days) plants. Lynch et al. (1981) reported that Florunner peanut was susceptible to FAW attack while other Arachis

species such as A. villosa and A. burkartii were resistant to this pest.

Pearl millet inbreds were screened as seedlings and approximately 4% (among 1436 inbreds) were rated resistant to first-instar FAW feeding (Leuck et al. 1968a). The highly nonpreferred millet inbred No. 240 was found to affect the development and the length of generations of FAW (Leuck 1970). Fertilizer effects were shown to influence FAW biology and the expression of host plant resistance for the given millet cultivar (Leuck 1972).

Leuck et al. (1968b) evaluated 441 clones of bermudagrass for their resistance to FAW; "Tifton 292" and "Tifton 296" were rated resistant, where 9 other clones were rated moderately resistant to larval feeding. Leuck and Skinner (1970) indicated that larval and pupal mortality were higher on those nonpreferred bermudagrass clones. Combs and Valerio (1980a) reared FAW on 4 varieties, i.e., common, "Coastal," "Callie," and "Alicia" of bermudagrass at 3 constant temperatures. They found that differences in length of larval period, pupal weight, and length of pupal period, between grasses were temperature- and sex-dependent. They also suggested that there was a possible direct relationship between oviposition preference of FAW and grass leaf size (Combs and Valerio 1980b). Lynch et al. (1983) reported a comparison of the effect of 9 bermudagrass clones on the biology of the FAW. By using a host-suitability index, "Tifton 44" was rated intermediately resistant and

"Tifton 292" was highly resistant to FAW feedings. The resistance in "Tifton 292" was primarily antibiosis.

Pencoe and Martin (1981, 1982a) investigated FAW development and preference on 15 grasses and sedges. They found that host diet significantly affected larval duration, number of instars, food consumption, and pupal weight. The most suitable hosts for FAW, as determined by a host-suitability index, were goosegrass, Eleusine indica (L.) Gaertn., and Coastal bermudagrass, while the least suitable host was yellow nutsedge, Cyperus esculentus L. (Pencoe and Martin 1982b). Wiseman et al. (1982) reported finding some of the highest resistance known to FAW in common centipedegrass, Eremochola ophiuroides (Munro) Hack. Both nonpreference and antibiosis resistance mechanisms were identified in centipedegrass.

CHAPTER III
FALL ARMYWORM HOST ORIENTATION AND PREFERENCE FOR SELECTED GRASSES

Introduction

The fall armyworm, Spodoptera frugiperda (J. E. Smith), damages not only important food and fiber crops, but often severely damages grasses grown for pasture, silage, turf, or soil conservation (Dew 1913, Kelsheimer et al. 1953, Koehler et al. 1977). The widespread distribution of these grasses makes them extremely important in the population dynamics of the FAW.

Chemical components in plants influence insect behavior in both food-finding and food-acceptance (Thorsteinson 1960). The chemicals may act as attractants, stimulants, repellents, or deterrents (Dethier et al. 1960) and influence insect behavior, including the preference or nonpreference mechanism of resistance as defined by Painter (1951). Numerous studies have been conducted for both chemical and nonchemical bases of food preference of lepidopterous larvae (Jermy et al. 1968, Chapman 1974, Hedin et al. 1977, Shorey and McKelvey 1977). However, the FAW has been studied less from an insect-plant relationship than many other economically important insect pests (Wiseman et al. 1967). The first part of this research, thus, was conducted to study

the FAW orientation and host preference mechanisms for selected grasses.

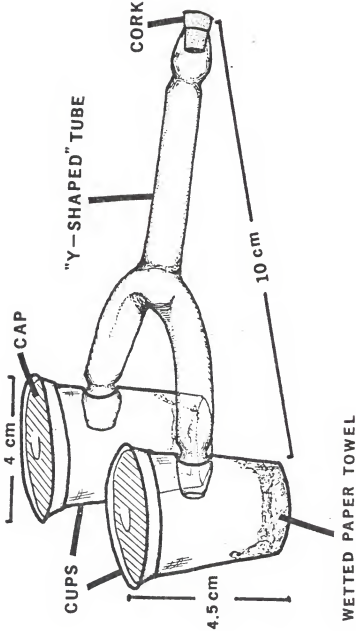
Materials and Methods

Coastal, Tifton 10, and Tifton 292 (P.I. 290884) bermudagrasses [Cynodon dactylon (L.) Pers.], C-181 and common centipedegrass [Eremochola ophiuroides (Munro) Hack.], and zoysiagrass (Zoysia sp.) were selected for the study. Plants of each grass were obtained from pure stands from the field and were subsequently maintained in a greenhouse for laboratory evaluations. The fall armyworm larvae used in the evaluation were obtained from a laboratory colony maintained at the Insect Biology and Population Management Research Laboratory (IBPMRL), USDA-ARS, Tifton, Georgia (Perkins 1979).

FAW Orientation

Orientation of FAW larvae to grass food sources was evaluated in an olfactometer constructed from two plastic rearing cups (4 cm diam, 4.5 cm high) connected with a 10 cm "Y-shaped" tube (Fig. 1). A wetted paper towel section was placed at the bottom of rearing cups to provide moisture. Grass clippings (4 g/sample) were placed in one or both of the rearing cups and the cups were capped. Twenty neonate FAW larvae were then placed in the entrance of the "Y-shaped" tube with a camel-hair brush after which the tube was sealed with a cork. The olfactometer was

Figure 1. Various components of the olfactometer used to evaluate the orientation of neonate fall armyworm.


CORK
"Y-SHAPED" TUBE
CAP
4 cm
10 cm
CUPS
4.5 cm
WETTED PAPER TOWEL

covered with dark paper to avoid phototactic influences on larval orientation. Data were recorded on the number of larvae in each rearing cup after 3 hr. Orientation comparisons of response of larvae included each individual grass vs. an empty cup and a one-on-one comparison for all grasses. Two replications with 5 olfactometers per replication of each comparison were conducted. Differences within each comparison were expressed in % FAW orienting to the respective stimuli. Data were evaluated with a t-test for paired comparisons.

Preference Tests

Two preference tests examined the responses of neonate FAW larvae to the 6 grasses. In the first test, larvae were presented a choice of all 6 grasses using the procedure described by Wiseman et al. (1982). Two leaf blades, each ca. 4.5 cm in length, were placed in a randomly paired fashion on moistened filter paper in the bottom of individual plastic dishes (25 cm diam.) before introducing 25 neonate FAW into the center of the dish. Six replications with 10 dishes per replicate were used. Data were expressed as the percentage of larvae on each grass.

The second test with neonate larvae was conducted to present the larvae with a choice of only 2 of the 6 grasses in each comparison. Two leaf blades of each of 2 selected grasses were placed opposite each other in a plastic feeding chamber, 8 cm in diam. x 2 cm deep. Five neonate

FAW larvae were then placed in the center of each dish and each dish was sealed with a lid. Twenty-four replications with one dish per replication were used in each comparison.

A third test was conducted to examine the preference of older FAW larvae for the 6 grasses. As in the first test, 25 cm diam. dishes were used in the evaluation and procedures were identical with the exception that 10 leaves of each grass were placed randomly in the 6 equal sections marked on the filter paper. Then 15 third-instar larvae were placed in the center of each dish for 4 replications with 6 dishes per replication. Dishes or feeding chambers in all 3 preference tests were sealed, covered with dark paper to exclude light influence, and placed in an incubator operated at 26.7 $\pm$ 2° C and 70 $\pm$ 5% RH. The number of larvae on or under each grass section was recorded at 12, 24, 36, and 48 hr. after infestation. Leaf damage was rated after 48 hr. on a 0-9 scale, where 0 = no damage and 9 = leaf totally consumed. The preferred ratio was obtained by calculating the mean percentage of larvae on each grass at each observation. The data were transformed (arcsin $\sqrt{\%}$) and subjected to an analysis of variance. The means were separated by Duncan's multiple range test (Duncan 1955).

Results and Discussion

FAW Orientation

In all 6 tests, when larvae were presented a choice of grass vs. an empty cup in the olfactometer, FAW

Table 1
Orientation of neonate fall armyworm (FAW) larvae
toward grass plant material vs. empty cups[1]

Plant material	% of FAW ($\bar{X} \pm$ SE) orienting to:		LSD (p=0.05)
	Grass	Empty cup	
Coastal bermudagrass	81.5 ± 7.6	4.5 ± 2.7	8.65
Common centipedegrass	74.5 ± 14.5	19.0 ± 11.8	20.01
Tifton 10 bermudagrass	76.0 ± 5.8	16.5 ± 6.9	9.63
Tifton 292 bermudagrass	83.5 ± 9.2	12.5 ± 8.3	13.32
C-181 centipedegrass	82.0 ± 6.6	6.5 ± 3.3	7.87
Zoysiagrass	79.5 ± 8.2	9.5 ± 6.8	11.39

[1]Data based on two replications with 5 observations for each replication.

orientation was significantly ($p < 0.05$) greater toward each individual grass (Table 1). During this test, larvae were observed to turn toward the cup that contained grass as they approached the Y-junction in the olfactometer. These observations and data demonstrate that chemoreception has an important role in host location by FAW neonate larvae and that chemotaxis is involved in this host orientation behavior.

When FAW larvae were presented a choice of 2 grasses, a significant ($p < 0.05$) difference in FAW orientation was noted in only 1 of the 15 paired comparisons (Table 2). The FAW larvae oriented significantly ($p < 0.05$) more toward Coastal bermudagrass than toward zoysiagrass. These results indicate that either (1) the host plants released the same or similar volatile chemicals or (2) they released different volatile chemicals that produced an equal response in oriented movement toward the hosts with the exception of Coastal bermudagrass vs. zoysiagrass. Also, there were no apparent repellent reactions associated with any of the 6 grasses.

Preference Tests

When larvae were presented a choice of all 6 grasses in the first preference test, Tifton 10 and Coastal bermudagrass were the most preferred ($p < 0.05$) by FAW neonate larvae over Tifton 292 bermudagrass, C-181 centipedegrass, and zoysiagrass at 24, 36, and 48 hr. (Table 3). The

Table 2
Orientation of neonate fall armyworm (FAW) larvae
in response to grasses in paired choices of six grasses[1]

Olfactometer containing			% FAW on host ($\bar{X}$ ± SE)			LSD (p=0.05)
Coastal bermudagrass	vs.	Common centipedegrass	43.0 ± 7.9	:	43.5 ± 10.3	13.94
Coastal bermudagrass	vs.	Tifton 10 bermudagrass	42.5 ± 6.1	:	41.0 ± 7.7	10.51
Coastal bermudagrass	vs.	C-181 centipedegrass	53.5 ± 12.4	:	36.5 ± 10.3	17.30
Coastal bermudagrass	vs.	Tifton 292 bermudagrass	47.0 ± 6.8	:	48.0 ± 5.3	9.32
Coastal bermudagrass	vs.	Zoysiagrass	58.5 ± 7.9	:	37.5 ± 8.2	12.16
Common centipedegrass	vs.	Tifton 10 bermudagrass	40.5 ± 9.9	:	39.5 ± 10.0	15.01
Common centipedegrass	vs.	C-181 centipedegrass	44.5 ± 14.4	:	51.5 ± 13.0	20.75
Common centipedegrass	vs.	Tifton 292 bermudagrass	40.0 ± 13.1	:	35.0 ± 5.5	15.26

Table 2--continued

Olfactometer containing			% FAW on host ($\bar{X} \pm$ SE)		LSD (p=0.05)
Common centipedegrass	vs.	Zoysiagrass	42.5 ± 10.8	42.0 ± 12.3	17.54
Tifton 10 bermudagrass	vs.	C-181 centipedegrass	45.5 ± 8.7	45.0 ± 7.0	11.97
Tifton 10 bermudagrass	vs.	Tifton 292 bermudagrass	42.0 ± 10.4	48.0 ± 10.9	16.08
Tifton 10 bermudagrass	vs.	Zoysiagrass	42.0 ± 8.7	51.0 ± 9.7	13.92
C-181 centipedegrass	vs.	Tifton 292 bermudagrass	47.5 ± 8.4	47.0 ± 8.4	12.80
C-181 centipedegrass	vs.	Zoysiagrass	46.5 ± 11.9	46.5 ± 9.1	16.10
Tifton 292 bermudagrass	vs.	Zoysiagrass	55.5 ± 11.9	41.5 ± 13.2	19.08

[1]Data based on two replications with 5 observations for each replication.

Table 3
Damage ratings and preference of fall armyworm (FAW) larvae for six grasses[1]

Grass	% FAW larvae on host at indicated hr. after infestation				Mean preferred ratio[2]	Damage rating[3]
	12	24	36	48		
Tifton 10 bermudagrass	20.7a	21.7a	16.4a	9.7a	10.6	4.8a
Coastal bermudagrass	11.9abc	12.5b	10.8b	9.3a	7.0	2.0b
Common centipedegrass	13.8ab	7.4bc	6.9bc	7.4ab	5.2	1.8bc
C-181 centipedegrass	5.6bc	3.9c	4.9cd	3.7bc	2.8	0.6bc
Tifton 292 bermudagrass	5.2bc	3.3c	2.5cd	3.1c	2.1	0.3c
Zoysiagrass	2.9c	1.3c	1.5d	1.3c	1.0	0.1c

[1]Means in a column not followed by the same letter are significantly different ($p=0.05$) by Duncan's multiple range test.

[2]Mean preferred ratio = Mean % FAW on specific grass / Mean % FAW on Zoysiagrass.

[3]Damage rating scale of 0 to 9, where 0 = no damage and 9 = leaf completely consumed.

results were expressed as a mean preferred ratio ($\bar{X}$ most preferred $\div$ $\bar{X}$ least preferred) and demonstrated that Tifton 10 was the most preferred while zoysiagrass was the least preferred. These mean preferred ratios closely paralleled damage ratings for the grasses. Tifton 10 bermudagrass sustained significantly ($p < 0.05$) more damage than any other grass, while zoysiagrass sustained the least damage, which was ca. 50-fold less than the damage of Tifton 10.

Results of the paired comparisons of grasses (second preference test) confirmed the results of the first preference test. Tifton 10 bermudagrass was preferred over all other grasses in a one-on-one comparison of preference (Table 4). Coastal bermudagrass was more preferred and had a significantly higher damage rating than common centipedegrass, thus confirming results reported by Wiseman et al. (1982). Coastal bermudagrass also was preferred over C-181 centipedegrass, zoysiagrass, and Tifton 292 bermudagrass.

Based on damage ratings and larval preference ratios, common centipedegrass was more preferred than C-181, Tifton 292 bermudagrass, or zoysiagrass. However, there was no significant difference in the damage rating between C-181 and common centipedegrass. Zoysiagrass was less preferred than C-181 and Tifton 292 bermudagrass. The differences between the less preferred grasses, such as C-181 centipedegrass vs. Tifton 292 bermudagrass and Tifton 292 bermudagrass vs. zoysiagrass, were more difficult to determine since the damage ratings of both comparisons were not

Table 4
Damage ratings and preference responses of neonate fall armyworm (FAW) larvae to paired comparisons of selected grasses[1]

Grass	% FAW larvae on host at indicated hr. after infestation				Mean preferred ratio[2]	Damage rating[3]
	12	24	36	48		
Tifton 10 bermudagrass	65.0a	56.1a	55.5a	42.5a	2.5	3.7a
vs.						
Coastal bermudagrass	25.5b	24.5b	23.5b	14.0b	1.0	1.0b
Tifton 10 bermudagrass	48.9a	33.5a	47.6a	23.9a	1.3	4.2a
vs.						
Common centipedegrass	24.6b	21.9b	21.7b	23.0a	1.0	1.0b
Tifton 10 bermudagrass	47.0a	51.7a	56.2a	31.6a	7.1	3.8a
vs.						
C-181 centipedegrass	8.8b	7.2b	6.2b	4.2b	1.0	0.3b
Tifton 10 bermudagrass	52.1a	59.6a	43.0a	35.6a	12.5	5.4a
vs.						
Tifton 292 bermudagrass	5.3b	3.1b	2.7b	4.1b	1.0	0.3b

Table 4--continued

Grass	% FAW larvae on host at indicated hr. after infestation				Mean preferred ratio[2]	Damage rating[3]
	12	24	36	48		
Tifton 10 bermudagrass	38.3a	31.7a	24.2a	24.2a	6.2	4.4a
vs.						
Zoysiagrass	6.7b	5.8b	2.5b	4.2b	1.0	0.2b
Coastal bermudagrass	50.4a	42.8a	48.4a	36.9a	3.3	3.9a
vs.						
Common centipedegrass	16.9b	12.7b	14.4b	10.2b	1.0	1.0b
Coastal bermudagrass	60.5a	53.0a	46.5a	29.0a	4.1	2.1a
vs.						
C-181 centipedegrass	16.5b	9.0b	11.0b	10.0b	1.0	0.3b
Coastal bermudagrass	58.4a	50.5a	48.6a	47.4a	7.3	3.1a
vs.						
Tifton 292 bermudagrass	7.7b	6.2b	6.9b	7.2b	1.0	0.1b

Table 4--continued

Grass	% FAW larvae on host at indicated hr. after infestation				Mean preferred ratio[2]	Damage rating[3]
	12	24	36	48		
Coastal bermudagrass vs. Zoysiagrass	36.5a 10.5b	26.5a 9.0b	32.5a 7.5b	17.5a 8.0b	3.2 1.0	0.7a 0.1b
Common centipedegrass vs. C-181 centipedegrass	36.3a 18.4b	34.6a 18.8b	30.0a 15.4b	22.5a 15.8a	1.8 1.0	0.9a 0.4a
Common centipedegrass vs. Tifton 292 bermudagrass	46.4a 4.7b	34.7a 3.9b	34.7a 6.4b	31.4a 5.0b	7.4 1.0	2.3a 0.1b
Common centipedegrass vs. Zoysiagrass	50.4a 5.0b	41.7a 2.5b	33.4a 1.7b	30.9a 0.9b	15.5 1.0	2.4a 0.1b

Table 4--continued

Grass	% FAW larvae on host at indicated hr. after infestation				Mean preferred ratio[2]	Damage rating[3]
	12	24	36	48		
C-181 centipedegrass	44.0a	44.0a	44.0a	28.0a	1.1	0.9a
vs.						
Tifton 292 bermudagrass	41.0a	28.0b	34.3a	37.0a	1.0	0.5a
C-181 centipedegrass	54.0a	46.0a	44.0a	28.0a	2.8	1.6a
vs.						
Zoysiagrass	4.0b	4.0b	4.0b	8.0b	1.0	0.3b
Tifton 292 bermudagrass	40.0a	30.0a	30.0a	26.0a	9.5	0.4a
vs.						
Zoysiagrass	11.0b	2.0b	0.0b	0.0b	1.0	0.1a

[1]Means within a column of each comparison not followed by the same letter are significantly different ($p=0.05$), by Duncan's multiple range test.

[2]Mean preferred ratio = Mean % FAW on most preferred grass / Mean % FAW on least preferred ones.

[3]Damage rating scale of 0 to 9, where 0 = no damage and 9 = leaf completely consumed.

significant and did not reflect feeding differences by the FAW larvae. Results were also confounded by high mortality during the tests that compared Tifton 292 bermudagrass and zoysiagrass.

Preferences of third-instar larvae for the various grasses were similar to the preferences exhibited by neonate larvae (Table 5). Tifton 10 bermudagrass was the most highly preferred at 12, 24, and 36 hr., had the highest mean preferred ratio, and sustained the most damage of all the grasses. Conversely, Tifton 292 bermudagrass and zoysiagrass were the least preferred, had the lowest preferred ratio, and sustained the least feeding damage. The FAW larval age, thus, had little influence on preference for the various grasses.

In comparing results of all three preference tests, the 6 grasses can be ranked in their order of preference by FAW larvae as follows: Tifton 10 bermudagrass is highly preferred; Coastal bermudagrass is moderately preferred; common and C-181 centipedegrass are moderately nonpreferred; Tifton 292 bermudagrass and zoysiagrass are highly nonpreferred. These results confirm the nonpreference of FAW for centipedegrass reported by Wiseman et al. (1982). Lynch et al. (1983) reported that the resistance of Tifton 292 bermudagrass to the FAW was primarily due to antibiosis. The results herein demonstrate that nonpreference is also a component of the resistance of this grass to the FAW.

Table 5
Preference of 3rd-instar fall armyworm (FAW) larvae for six grasses[1]

Grass	% FAW larvae on host at indicated hr after infestation				Mean preferred ratio[2]	Damage rating[3]
	12	24	36	48		
Tifton 10 bermudagrass	35.9a	11.7a	20.0a	6.6ab	9.1	8.2a
Coastal bermudagrass	15.0b	5.9bc	11.9b	10.4a	5.3	4.9b
Common centipedegrass	15.5b	8.6ab	10.3b	7.1ab	5.1	3.3c
C-181 centipedegrass	6.9c	4.2c	7.3b	5.9bc	3.0	1.3d
Tifton 292 bermudagrass	2.8c	1.7d	2.2c	1.5d	1.0	0.3d
Zoysiagrass	2.2c	5.0c	2.5c	3.3cd	1.6	0.3d

[1]Means in a column not followed by the same letter are significantly different ($p=0.05$) by Duncan's multiple range test.

[2]Mean preferred ratio = Mean % FAW on specific grass / Mean % FAW on Tifton 292 bermudagrass.

[3]Damage rating scale of 0 to 9, where 0 = no damage and 9 = leaf completely consumed.

Dethier (1937) indicated that the senses of taste and smell are of vital importance in the selection of host plants by lepidopterous larvae. In the above tests, FAW larvae initially showed a random movement followed by an oriented movement toward the host in response to chemical cues emanating from the host. However, the rejection or acceptance of these grass hosts by FAW larvae occurred only after they located the grass and fed on it. Coastal bermudagrass (Leuck and Skinner 1970) and Tifton 10 bermudagrass used in this study were susceptible to FAW feeding while centipedegrass (Wiseman et al. 1982), zoysiagrass (unpublished), and Tifton 292 bermudagrass (Leuck et al. 1968b, Lynch et al. 1983) were resistant. However, the preference or nonpreference for these grasses as hosts occurred after the FAW larvae perceived the presence of the grass through chemoreception, moved toward the grass, and began feeding.

CHAPTER IV
THE INFLUENCE OF NITROGEN FERTILIZER APPLICATION ON THE RESISTANCE OF GRASSES TO FALL ARMYWORM

Introduction

The interrelationship of soil fertility and plant resistance to insects is of vital importance in the management of insects (Tingey 1981). Numerous studies indicate that fertilizers affect growth, survival and fecundity of insects (Painter 1951, Rodriguez 1960, Singh 1970, Tingey and Singh 1980).

The nutritional content (i.e., N, P, K, etc.) of various host crops of FAW larvae can influence the expression of plant resistance. Leuck (1972) applied 7 fertilizer treatments to pearl millet [Pennisetum typhoides (Berm.) Stapf and C. E. Hubb] cultivar "Gahi" and found high non-preference and low antibiosis for the FAW larvae feeding on NPK- and NP- treated plants, respectively. Wiseman et al. (1973a) found that additions of N to any combination of NPK greatly increased the susceptibility of "Antigua" corn foliage to FAW larval feeding. Moreover, Wiseman et al. (1973b) indicated that corn treated with N fertilizer was the most susceptible to this pest. Leuck et al. (1974) showed that 14 inorganic compounds sprayed on the foliage of Coastal bermudagrass, corn, or sorghum could deter FAW

larval feeding. Also Leuck and Hammons (1974a, 1974b) showed that fertilizer can cause significant variation in the resistance of peanut cultivars to FAW feeding.

Martin et al. (1980) reported that Coastal bermudagrass was particularly susceptible to FAW when pastures were heavily fertilized. Lynch (1984) showed that increasing the nitrogen fertilizer application on Coastal bermudagrass had a significant effect on the biology of FAW larvae. However, the effects of fertilizer on FAW larval host orientation, feeding response, and host selection have not been addressed in previous studies. Thus, the present study reports the influence of nitrogen fertilization on the expression of resistance or susceptibility to FAW in Coastal bermudagrass and common centipedegrass.

Materials and Methods

Coastal bermudagrass and common centipedegrass were collected and planted in pots (12 cm diam, 12.5 cm high) in the greenhouse. Initially, the grass in each pot was fertilized with 5 g ammonium nitrate (34% nitrogen and ca. 376 kg N/ha) on July 1, 1983. The pots for each grass were then equally divided, and one-half of the pots received no additional fertilization and were designated NB and NC for the nonfertilized bermudagrass and centipedegrass, respectively. The remaining pots of grass were fertilized every 2 weeks throughout the study with 5 g ammonium nitrate to maintain a high level of fertilization; these treatments

were designated FB and FC for the fertilized bermudagrass and centipedegrass, respectively.

Preference Tests

Experiment 1 was designed to compare the preference of neonate FAW larvae for NC vs. FC and NB vs. FB. Foliage was excised from each treatment 15, 30, and 40 days after the first fertilizer application and evaluated for feeding responses of FAW larvae. The experiment included 3 replications with 12 observations per replicate and was designed in a split-split plot in a randomized complete block with grass as the whole plot, fertilization vs. no fertilization as the subplot and time interval after initial fertilization as the sub-subplot. Two excised leaf blades (ca. 4 cm long) from each treatment were placed oppositely in a plastic feeding chamber (8 cm diam, 2 cm high). Ten neonate larvae were then placed in the center of each chamber, and the chamber was covered with a tight fitting plastic cover. The chambers were then placed in an incubator operated at 26.7 $\pm$ 2° C and 70 $\pm$ 5% RH and covered with dark paper to prevent phototactic influence. Data were recorded on the mean number of larvae on each treatment at 12, 24, 36, and 48 hr. after infestation. Damage was recorded at 48 hr. after infestation based on a visual rating scale from 0 to 9 where 0 = no damage and 9 = leaf completely consumed. These data were subjected to an analysis of variance, and means were separated by Duncan's multiple range test.

A second experiment was conducted to evaluate the preference of third-instar FAW larvae. The experimental design was identical to that described for Experiment 1. Ten excised leaves of each treatment combination were placed on a moistened filter paper disc along the outer edge of a 25.4 cm diam plastic dish in a randomized complete block design for each of 15 replications. Ten third-instar FAW larvae previously fed on a pinto bean diet (Burton 1967, Perkins 1979) were placed in the center of each dish, and they had a choice of the 12 grass-fertilizer-age treatment combinations on which to feed. Data were recorded and analyzed, and means were separated as described for the first test.

Antibiosis Tests

The first experiment for antibiosis was a randomized complete block design (RCBD) with 36 replications. The FAW larvae were confined, individually, in plastic cups (5 cm diam, 3.5 cm high) and fed excised foliage from NC, NB, FC, or FB. The test was initiated 20 days after the first application of fertilizer. Five leaf sections of the appropriate treatment combination were placed in each of 36 plastic cups with moist filter paper in the bottom. Each cup was infested with 1 neonate FAW larvae. The cups containing larvae were then placed in an incubator maintained as described above. Data were recorded on larval weights at 5, 7, and 9 days after infestation, number of days to complete larval development, pupal weight, and survival.

The second antibiosis experiment was conducted to evaluate the influence of the fertilized and nonfertilized grass when the grass was incorporated into a standard pinto bean diet (Burton 1967, Perkins 1979). The experiment was also a RCBD with 36 replications. Twenty grams (fresh wt.) of NC, NB, FC, or FB were blended into 300 ml of pinto bean diet plus 80 ml of water for 3 min. The mixture was dispensed into 36 one-oz plastic cups and allowed to solidify and cool. One neonate FAW larvae was then placed in each cup, the cups were capped, and then placed in an incubator operated as previously described. Data were recorded on the larval weights at 5, 7, and 9 days after infestation and on larval survival. The data of the antibiosis tests were analyzed and means were also separated by Duncan's multiple range test.

Results and Discussion

Preference Tests

Table 6 presents the results of the preference test that compared NC vs. FC and NB vs. FB at 15, 30, and 40 days after initial fertilization. Both the number of larvae on excised foliage and the leaf damage rating of FC were significantly ($p < 0.05$) greater than the number of larvae on or damage of NC during all three observational periods. The number of FAW larvae preferring NC declined significantly from 30 to 40 days after fertilization, and the damage rating declined significantly on NC during each of the three observational periods. Conversely, preference for and

Table 6

Preference of neonate fall armyworm (FAW) larvae for nonfertilized common centipedegrass (NC) vs. fertilized common centipedegrass (FC) and nonfertilized Coastal bermudagrass (NB) vs. fertilized Coastal bermudagrass (FB)[1]

Days after initial fertilization	Common centipedegrass						Coastal bermudagrass					
	No. of FAW			Damage rating[2]			No. of FAW			Damage rating[2]		
	NC	VS	FC	NC	VS	FC	NB	VS	FB	NB	VS	FB
15	2.1a	*	3.9a	2.9a	*	5.1b	2.5a		2.4b	2.9a		2.8a
30	1.7a	*	4.2a	1.3b	*	7.2a	0.8b	*	5.1a	0.3b	*	4.6a
40	0.4b	*	3.7a	0.3c	*	4.8b	0.3b	*	4.5a	0.1b	*	4.6a

[1]Means within a vertical column followed by different letters or marked with an * within each horizontal comparison are significantly different at $p=0.05$, by Duncan's multiple range test.

[2]Damage rated on a 9-0 scale where 0 = no damage and 9 = leaf completely consumed.

damage on FC remained relatively high during the three observational periods. By the end of the test, larvae showed a 9-fold preference for FC compared with NC, and damage on FC was 16 times greater than on NC.

On the susceptible Coastal bermudagrass, there were no significant differences between NB and FB in preference or damage rating at 15 days. However, on the 30 and 40 days observation periods, FB was significantly preferred over NB, and damage was significantly greater on FB than on NB. The number of larvae choosing FB actually increased and damage remained high over time. Conversely, on NB the preference and damage declined rapidly over time. Larvae showed a 15 times increase in preference for FB and a 46 times increase in damage on FB compared with NB.

These data suggest that preference for the FAW-resistant common centipedegrass increases with N-fertilization and that preference for the susceptible Coastal bermudagrass declines without fertilization. However, the opposite is the accepted production practice, i.e., centipedegrass normally requires very little fertilization while bermudagrass is normally highly fertilized. Lynch (1984) reported that damaging FAW infestations in Coastal bermudagrass are usually found in well-managed, highly fertilized pastures for hay, whereas poorly managed pastures for cattle grazing seldom have economic FAW infestations. Thus, the expressions measured for FAW on NC and FB would more nearly duplicate the normal agricultural practices.

The second preference experiment was designed to test the preference of third-instar FAW larvae by permitting them a free choice of NC, FC, NB, and FB (Table 7). At 15 days FC was the most preferred, as evidenced by the number of larvae on leaf blades. At 30 and 40 days the larvae significantly ($p < 0.05$) preferred FC and FB over NC and NB and caused significantly more damage on the leaf blades of both FC and FB compared with NC and NB. The FC was actually significantly preferred over FB at 30 days. This may be due to a more rapid N-uptake by centipedegrass vs. bermudagrass. However, as the period after initial fertilization increased, the number of larvae and damage decreased on NC and NB. Both FC and FB were preferred and received heavy leaf damage at all 3 observation times.

The results of the preference tests indicate that the preference of FAW larvae for either the resistant centipedegrass or susceptible bermudagrass was due in part to the fertilization level. Centipedegrass is normally nonpreferred, but preference for this grass can be increased with fertilization. Coastal bermudagrass is normally susceptible to FAW larval feeding, but preference can be reduced by lack of fertilization. These results are similar to those reported by Wiseman et al. (1973a) who indicated nitrogen fertilization increased FAW preference for FAW-resistant "Antigua" corn.

Table 7
Preference of 3rd-instar fall armyworm (FAW) larvae for nonfertilized (NC), fertilized common centipedegrass (FC), nonfertilized (NB), and fertilized Coastal bermudagrass (FB)[1,2]

Treatment	No. of FAW at			Damage rating[3] at		
	15 DAF[4]	30 DAF	40 DAF	15 DAF	30 DAF	40 DAF
NC	1.0c X	0.6c Y	0.5b Y	2.4b X	1.0c Y	0.4c Z
FC	1.9a X	1.7a XY	1.6a Y	4.5a X	5.1a X	4.7b X
NB	1.1bc X	0.6c Y	0.4b Y	2.9ab X	0.5c Y	0.1c Y
FB	1.4b X	1.3b X	1.7a X	4.0ab X	3.5b Y	6.5a X

[1]Means within a column followed by the same lowercase letter and means within a horizontal line followed by the same capital letter are not significantly different at $p=0.05$, by Duncan's multiple range test.

[2]Data based on 3 replications with 5 observations/replicate.

[3]Damage rated on a 0-9 scale where 0 = no damage and 9 = leaf completely consumed.

[4]DAF = days after the first fertilizer application.

Antibiosis Tests

Table 8 presents the results of the antibiosis experiment where FAW larvae were fed foliage of only one of the four grass treatments, i.e., force-fed throughout the larval stage. All of the insects died after feeding for only 7 days on the leaf blades of NC. This high larval mortality may be caused by an extreme nonpreference, a feeding deterrent, and/or toxic chemicals within the foliage of NC. The weight of FAW larvae fed on FC was slightly but not significantly less than those larvae that fed on NB and FB at 5 and 7 days after infestation. At 9 days, larvae fed FB weighed significantly more than larvae fed either FC or NB. However, the development of larvae that fed on FC was significantly delayed ca. 3 days. Thus the N application may mask the resistance factor(s) which are expressed in unfertilized common centipedegrass, but does not mask the antibiosis effect that retards larval development.

Female pupae produced from larvae that fed on NB weighed significantly less than larvae that fed on FB. This finding is in agreement with that found by Lynch (1984). However, except for the 100% mortality of insects reared on NC, there were no significant differences in the survival rate of FAW which fed on FC, NB, or FB. In this experiment, the greatest FAW damage occurred on bermudagrass at the higher frequency of N fertilization supporting the observation by Martin et al. (1980). If the cultural manipulations of the FAW in Coastal bermudagrass by applying N by 1 June

Table 8
Effects of force-feeding fall armyworm larvae on nonfertilized (NC), fertilized common centipedegrass (FC), nonfertilized (NB), and fertilized Coastal bermudagrass (FB)[1]

Treatment	Larval wt. (mg) at			Length of larval period (days)	Pupal wt. (mg)		% survival to adult emergence
	5 DAI[2]	7 DAI	9 DAI		Female	Male	
NC	1.1b	-	-	-	-	-	0.0b
FC	8.5a	28.4a	78.4b	16.7a	134.8b	141.1a	80.0a
NB	9.6a	29.0a	76.4b	13.2b	135.1b	137.0a	83.4a
FB	10.0a	32.9a	103.4a	13.9b	170.3a	153.7a	86.7a

[1]Means within each column, followed by the same letter, are not significantly different at $p=0.05$, by Duncan's multiple range test.

[2]DAI = Day after infestation.

to produce > 80% of annual yield by 1 August could be practically developed as suggested by Lynch et al. (1980), then large populations of this pest could be avoided by decreasing the heavy N fertilization later in the season.

Wiseman et al. (1984) tested the FAW with the standard pinto bean diet mixing different concentration levels of Coastal bermudagrass or common centipedegrass. They found that centipedegrass significantly decreased growth of larvae compared to Coastal bermudagrass at all tested concentrations. Similarly, in the second antibiosis experiment herein, FAW larvae developed more slowly on the NC- and FC-diet mixtures, as indicated by the significantly ($p < 0.05$) lower larval weights compared to those fed on the bermudagrass-diet mixture or the check diet at 5 and 7 days after infestation (Table 9). There were no significant differences in the larval survival rate between FAW fed on all the grass-diet mixtures (86.1 - 94.4%) and those fed on pinto bean check diet (97.2%).

It was observed that after NC- and FC-diet mixtures were dispensed and cooled, an unknown material, brown in color, appeared on the diet surface. This material was believed to be the oxidized chemical(s) from the leaf tissue and thus may be the factor(s) that inhibit feeding by FAW larvae. Similar reactions were observed by Wilson et al. (1984) when they mixed resistant corn silk into various meridic diets. Wiseman (personal communication) also observed this phenomenon for Tripsacum incorporated into a

Table 9
Larval weight and percentage survival of fall armyworm when fed pinto bean diet mixed with the foliage of nonfertilized (NC), fertilized common centipedegrass (FC), nonfertilized (NB), or fertilized Coastal bermudagrass (FB)[1]

Treatment	Larval wt. (mg) at 5 DAI[2]	7 DAI	9 DAI	Survival to pupation (%)
Pinto bean diet + NC	11.0b	54.4b	185.0b	94.4a
Pinto bean diet + FC	11.9b	58.9b	200.6ab	94.4a
Pinto bean diet + NB	17.4a	89.5a	253.3a	86.1a
Pinto bean diet + FB	17.2a	89.5a	257.9a	91.7a
Pinto bean diet (Check)	17.5a	83.9a	225.7ab	97.2a

[1]Means within each column, followed by the same letter, are not significantly different at $p=0.05$, by Duncan's multiple range test.

[2]DAI = Day after infestation.

meridic diet for FAW evaluations. Thus, this unknown material that forms on the diet surface when centipedegrass is incorporated may be responsible for the delayed larval development (Table 8) and reduced larval weights (Table 9). However, this chemical(s) must be isolated, identified, and bioassayed against FAW larvae before a conclusive statement is made.

CHAPTER V
EXPRESSIONS OF ANTIBIOSIS IN SELECTED GRASSES

Introduction

The different species of plants, even different varieties of the same plant species, could dramatically influence the development of FAW. Considerable biological variation can be seen when the FAW was reared on corn (Keller 1980, Wiseman et al. 1981), peanuts (Leuck and Skinner 1971, Garner and Lynch 1981, Lynch et al. 1981), cotton, corn, and soybean (Pitre and Hogg 1983).

Variations in FAW development have also been noted on different grasses. Leuck and Skinner (1970) reported higher larval and pupal mortality, reduced pupal weight and a shorter life cycle for FAW larvae fed "Tifton 239" than for those fed "Coastal" bermudagrass. Pencoe and Martin (1981, 1982a) reared FAW on 15 grasses or sedges and found that the host plant significantly affected FAW larval development rate, number of larval instars and pupal weight. Wiseman et al. (1982) also noted that FAW larvae fed common centipedegrass had significantly lower larval weights than when they were fed Coastal bermudagrass. Combs and Valerio (1980a) reported a more rapid larval development, heavier pupae, and longer adult female longevity on "common"

bermudagrass than on "Alicia" bermudagrass. Moreover, Lynch et al. (1983) compared the biology of the FAW on 9 different varieties of bermudagrass, and noted that "Tifton 68" and "Tifton 84" were the most suitable hosts for FAW development due to more rapid development rate, lower leaf consumption, higher pupal weights, and higher survival rates on these two varieties. Conversely, based upon the extremely low larval weight gain and high mortality, "Tifton 292" was rated as highly resistant to FAW (Lynch et al. 1983).

The adverse effects exerted by a plant on an insect's biology, defined as "antibiosis" by Painter (1951), is a basic method to evaluate insect resistance in plants (Dahms 1972). Thus, the third part of this research is the evaluation of selected grasses, ranging from resistant to susceptible, as hosts for the FAW, to more clearly define their antibiosis to the FAW.

Materials and Methods

Six different grasses, i.e., "Coastal," "Tifton 10," and "Tifton 292" bermudagrass, common centipedegrass, zoysiagrass, and corn were selected in this study. Cultures of each grass were maintained in the greenhouse and fertilized ca. every 2 weeks with 5 g ammonium nitrate (34% nitrogen available). Corn leaf blades were excised from plantings of open-pollinated Pioneer 3369A maintained at IBPMRL experimental farm.

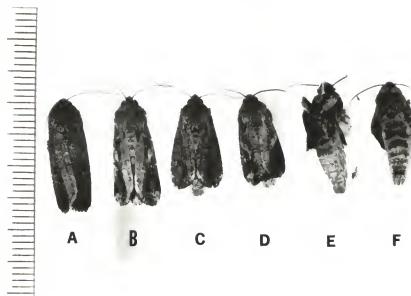
Test 1

Five to 10 leaf sections (ca. 4-5 cm long) of selected grass were placed in each of 30 plastic cups (5 cm diam, 3.5 cm high) containing wet filter paper in the bottom to provide moisture. Cups for each grass treatment were then infested with 1 neonate FAW per cup. An additional group of 30 cups containing pinto bean diet (Burton 1967, Perkins 1979) were also infested with 1 larva per cup for comparison. The test was a randomized complete block design (RCBD) with 30 replications. The grass within the cups was replaced every day, and the entire experiment was maintained in an incubator at 26.7 $\pm$ 2° C, 70 $\pm$ 5% RH and a photoperiod of LD 14:10. Data were recorded on larval weight at 5, 7, and 9 days after infestation, number of days to complete larval development, pupal weight (at 24 hr. old), pupal duration, and percent survival to adult emergence. All the data were subjected to an analysis of variance, and group means were compared by Duncan's multiple range test.

Test 2

The second test was conducted to evaluate the antibiosis effects of selected grasses to FAW when the grass was incorporated into the standard pinto bean diet (Burton 1967, Perkins 1979). This test was also designed as a RCBD with 36 replications. Corn and Tifton 10 bermudagrass were excluded in this test because they showed no antibiosis effect in Test 1.

Figure 2. The wing characteristics of fall armyworm after feeding larvae on pinto bean and grass-mixture diets. A, B, Normal female and male adult. C, D, Female and male adult showing minor wing deformity. E, F, Female and male showing major wing deformity.


A
B
C
D
E
F

Twenty grams (fresh wt.) of selected grass were blended into 300 ml of pinto bean diet plus 80 ml of water for 3 min. The mixture was dispensed into 36 one-oz plastic cups and allowed to solidify and cool. Also, 80 ml of water was added to a pinto bean diet check and blended 3 min. One neonate FAW larva was then placed in each cup, the cups were capped, and placed into the incubator operated as previously described. In addition to the data recorded as Test 1, the percentage of moths having major wing deformities was also recorded. These included moths with wings that were seriously stunted, twisted, and incapable of flight (Fig. 2 E, F). The statistical methods utilized to analyze the data and separate the means were as described for Test 1.

Results and Discussion

The effects of the selected grasses on FAW larval development in comparison with the laboratory diet are presented in Table 10. Initially, FAW larvae gained weight significantly more rapidly on corn and Tifton 10 bermudagrass than on pinto bean diet. However, by 7 days larval weight gain was significantly greater on the pinto bean diet than for any other treatment. During all 3 observations, weights of larvae fed on corn and Tifton 10 bermudagrass were significantly greater than weights of larvae fed on any of the other grasses. Similarly, weights of larvae fed on Coastal bermudagrass and common centipedegrass were

Table 10
Fall armyworm larval weight gain and larval duration when confined on selected grasses or pinto bean diet[1,2]

Host diet	Larval wt. (mg) at indicated days after infestation			Larval duration (days)
	5	7	9	
Pinto bean diet	18.7 ± 4.9b	141.5 ± 35.5a	404.9 ± 98.5a	11.5 ± 0.5e
Corn	23.8 ± 15.5a	90.0 ± 35.9c	225.5 ± 58.0b	12.2 ± 1.0d
Tifton 10 bermudagrass	23.8 ± 9.6a	110.0 ± 30.7b	224.4 ± 61.6b	12.6 ± 1.8d
Coastal bermudagrass	10.0 ± 4.0c	31.3 ± 13.0d	93.5 ± 36.2c	14.8 ± 1.3c
Common centipedegrass	8.5 ± 4.1c	28.4 ± 13.0d	78.4 ± 33.3c	16.7 ± 1.5b
Tifton 292 bermudagrass	2.4 ± 1.1d	6.4 ± 3.1e	15.7 ± 8.0d	20.8 ± 1.7a
Zoysiagrass	-	-	-	-

[1]Data expressed as Mean ± 1 SD.

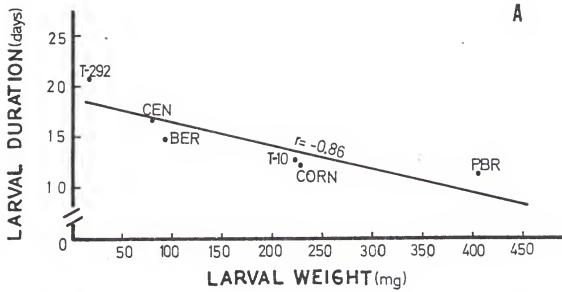
[2]Means within each column not followed by the same letter are significantly different at $p=0.05$ level by Duncan's multiple range test.

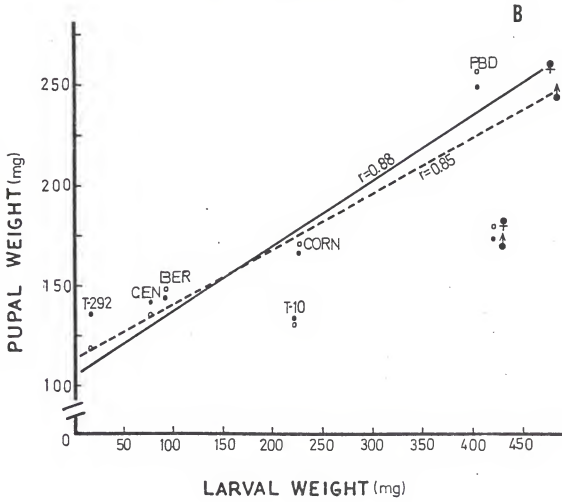
significantly heavier than weights of larvae fed on Tifton 292 bermudagrass. All larvae on zoysiagrass died within 2 days. At 9 days, weights of larvae were 14 to 25 times greater on more suitable hosts, i.e., pinto bean diet, corn, and Tifton 10 bermudagrass, than on Tifton 292 bermudagrass, and 3 to 5 times greater on these hosts than on Coastal bermudagrass or common centipedegrass.

The rapid weight gain on the more suitable hosts resulted in a decrease in time required to complete larval development (Fig. 3 A). The significant correlation ($r = -0.86$, $p < 0.05$) showed that a rapid larval weight gain on the most suitable hosts significantly reduced the number of days needed to complete larval development. Moreover, it was observed that FAW larvae required only the normal 6 instars to complete larval development on the more suitable hosts (corn, Tifton 10 bermudagrass and diet) while 6 or 7 molts were required on less suitable hosts (common centipedegrass and Tifton 292 bermudagrass). Thus, it appears that the relatively slow larval weight gain on the less suitable hosts had a cumulative resistant effect by increased time for larval development. However, this increased time also allowed FAW larvae to reach the minimum weight needed for larval pupation.

Pupal weights were also significantly affected by larval host (Table 11). Both male and female pupae from larvae that fed on the pinto bean diet were significantly heavier than pupae from larvae on the grass hosts.

Figure 3. Relationship between mean larval duration and larval weight (A), pupal weight and larval weight (B), for fall armyworm larvae feeding on various host diets 9 days; where BER = Coastal bermudagrass, CEN = common centipedegrass, PBD = pinto bean diet, T 10 = Tifton 10 bermudagrass, T 292 = Tifton 292 bermudagrass.


A
LARVAL DURATION (days)
25
20
15
10
0
T-292
CEN
BER
r= -0.86
T-10
CORN
PBR
50
100
150
200
250
300
350
400
450
LARVAL WEIGHT (mg)


B
PUPAL WEIGHT (mg)
250
200
150
100
0
PBD
r=0.88
r=0.85
CORN
BER
CEN
T-292
T-10
50
100
150
200
250
300
350
400
450
LARVAL WEIGHT (mg)

Similarly, male and female pupae from larvae that fed on corn were significantly heavier than pupae from the other hosts. Female pupal weights were also significantly greater for larvae that fed on Tifton 10, Coastal bermudagrass or centipedegrass than for larvae that fed on Tifton 292 bermudagrass. However, with the exception of Tifton 292, there were no significant differences between male and female pupal weights on a given host.

Both male and female pupal weights were highly correlated ($r = 0.88$ and 0.85, $p < 0.05$) with larval weight gain at 9 days (Fig. 3 B). Thus, the FAW that fed on the more suitable hosts not only exhibited faster weight gain and shorter larval duration, but also produced heavier pupae. Furthermore, the delayed larval development on the less suitable hosts, Tifton 292 and centipedegrass, was not sufficient for complete compensation for the slower weight gain and resulted in significantly smaller pupae than for the more suitable corn or pinto bean diet.

Larval hosts did not influence pupal development (Table 11). There were no significant differences in time to complete pupal development for either males or females that were related to larval hosts. However, female pupal duration was significantly shorter ($p < 0.05$) than male pupal duration on all hosts except Tifton 292.

Survival to adult emergence was drastically influenced by larval hosts (Table 11). Survival was greatest on the pinto bean diet, as might be expected, since this diet is

Table 11
Pupal weights, pupal duration and percent survival of fall armyworm confined on pinto bean diet or selected grasses[1,2]

Host diet	Pupal wt. (mg)		Pupal duration (days)		% survival to adult emergence
	Female	Male	Female	Male	
Pinto bean diet	255.6 ± 18.1a	249.4 ± 15.2a	8.0 ± 0.8a *	8.8 ± 0.4a	96.7a
Corn	171.1 ± 39.5b	166.7 ± 20.7b	8.0 ± 0.9a *	8.6 ± 0.7a	76.7b
Tifton 10 bermudagrass	131.3 ± 17.4c	133.2 ± 19.7c	7.5 ± 0.7a *	8.1 ± 1.0a	83.3b
Coastal bermudagrass	148.0 ± 26.2c	143.5 ± 22.5c	7.9 ± 0.6a *	8.7 ± 0.8a	80.0b
Common centipedegrass	134.8 ± 18.5c	141.1 ± 19.2c	8.0 ± 0.7a *	8.9 ± 0.7a	80.0b
Tifton 292 bermudagrass	111.8 ± 4.8d *	135.6 ± 14.9c	8.3 ± 0.5a *	9.0 ± 0.0a	20.0c
Zoysiagrass	-	-	-	-	0.0d

[1]Data expressed as Mean ± 1 SD.

[2]Means within a vertical column followed by different letters or marked with an * within each horizontal comparison are significantly different at $p=0.05$, by Duncan's multiple range test.

routinely used to rear the FAW in the laboratory. Survival on corn, Tifton 10, Coastal, and centipedegrass was ca. 80%. Only 20% of the larvae on Tifton 292 bermudagrass survived to adult emergence. Zoysiagrass is essentially immune to FAW feeding and none of the larvae survived. This is the first report on the extremely high level of resistance of zoysiagrass to FAW.

The data from the second antibiosis test of FAW larvae that were fed on selected grass foliage incorporated into the pinto bean diet are shown in Table 12. The FAW larvae, again, weighed significantly more when fed the pinto bean diet than on the grass-diet mixtures at 5 days after infestation. The larvae developed more slowly when they were fed common centipedegrass-diet mixture, as indicated by the significantly lower larval weights at 7 days after infestation and longer time required for completion of the larval development (11.9 days). The slower larval development of FAW larvae fed on this mixture was possibly caused by some oxidized chemical(s) on the diet surface from common centipedegrass leaf tissue as described in Chapter IV. These chemical(s) might possibly be the factor(s) that inhibit the feeding of FAW larvae.

The antibiosis effects of Tifton 292 bermudagrass and zoysiagrass were shown by the lower larval weights 9 days after infestation and by lower pupal (both female and male) weights when these two grasses were incorporated into the pinto bean diet. However, similar to the results of Test 1,

Table 12
The biological responses of fall armyworm larvae fed on pinto bean (PBD) and grass mixture diet[1,2]

Treatment	Larval Wt (mg) at 5 DAI[3]	Larval Wt (mg) at 7 DAI	Larval Wt (mg) at 9 DAI	Larval Duration (Days)	Pupal Wt (mg) Female	Pupal Wt (mg) Male	Pupal Duration (Days) Female	Pupal Duration (Days) Male	% Survival to Adult Emergence	% Adult Showing Wing Deformity
Pinto Bean diet (CK)	26.1a	135.7a	417.6a	11.6ab	276.4a	254.9a	7.9a	8.7b	97.2a	2.9a
	(8.7)	(27.7)	(84.1)	(0.6)	(24.2)	(26.2)	(0.6)	(0.5)		
PBD+Coastal bermudagrass	21.6b	125.1a	389.1a	11.4b	264.8a	262.1a	8.1a	9.0b	94.4a	3.1a
	(8.2)	(26.4)	(76.1)	(0.6)	(27.5)	(18.8)	(0.5)	(0.3)		
PBD+Common centipedegrass	21.1b	101.8b	314.4b	11.9a	267.7a	261.9a	8.1a	9.0b	86.1ab	10.3b
	(7.9)	(31.9)	(84.8)	(0.9)	(14.7)	(16.7)	(0.5)	(0.4)		
PBD+Tifton 292 bermudagrass	18.8b	131.0a	331.4b	11.1b	229.7b	234.2b	8.0a	9.4a	82.4ab	14.3b
	(8.6)	(47.7)	(121.6)	(1.6)	(52.3)	(23.5)	(0.7)	(0.7)		
PBD+Zoysia grass	22.8b	127.9a	338.5b	11.1b	237.3b	219.4b	8.1a	8.6b	77.8b	3.6a
	(8.6)	(35.6)	(110.8)	(1.2)	(20.9)	(15.6)	(0.8)	(1.1)		

[1] Data expressed as Mean ± 1 (SD).

[2] Means within a vertical column followed by different letters are significantly different at p = 0.05 by Duncan's multiple range test.

[3] DAI = Day after infestation.

there were no significant differences in developmental time to the pupal stage when larvae were reared on the grass-diet mixtures. The high antibiosis effect of zoysiagrass was also shown by the significantly high mortality when the larvae were fed on the zoysiagrass-diet mixture. During the pupal stage, 17.6% of the FAW died with serious wing-area deformities (Fig. 4). Although there were no significant differences in percentage survival of FAW when larvae were reared on centipedegrass-diet and Tifton 292-diet mixture as compared to other treatments, significantly more adults showed major wing deformity (Fig. 2 E, F).

Based on the nutritional investigations, the factors required for optimal larval growth and normal wing development have been studied for several phytophagous insects. In general, at least three nutritional components have been shown to be required for normal wing development when the lepidopterous insects were fed on artificial diet. First, wheat germ was necessary for normal wing development of the cabbage looper, Trichoplusia ni (Chippendale et al. 1965). Second, polyunsaturated fatty acids (especially linolenic and linoleic acid) could alleviate wing deformity of certain lepidopterous insects (Fraenkel and Blewett 1946, Vanderzant et al. 1957, Dadd 1964, Chippendale et al. 1965, Levinson and Navon 1969). Third, ascorbic acid (vitamin C) appeared to be important in the normal wing development of the salt-marsh caterpillar, Estigmene acrea (Drury) (Vanderzant et al. 1962). Only 2.9% of wing deformities of FAW

Figure 4. The abnormal fall armyworm pupae with wing area deformities after feeding larvae on pinto bean and resistant grass-mixture diet.

occurred when larvae were reared on pinto bean diet (Table 12). The serious wing lesions that developed when FAW were reared on centipedegrass- and Tifton 292-diet mixtures, and the abnormal pupae with wing-area deformities that occurred when they were reared on zoysiagrass-diet mixtures should not have been caused by a lack of necessary nutrient(s) for the wing formation. It was believed that certain secondary plant chemical(s) in the resistant grasses adversely affected normal wing formation.

A suitable host for an insect is characterized by high insect survival, rapid insect development and high pupal weight. As noted by Lynch et al. (1983), survival is paramount in this relationship since survival results in propagation of the species. Pupal weight is also very important since it is related to fecundity (Leuck and Perkins 1972). The FAW larvae fed on pinto bean diet and corn, gained weight rapidly, required a shorter period of time to complete larval development, and obtained greater pupal weights (Tables 10, 11, 12). Thus, these foods would be classified as highly suitable. Using these same criteria, Tifton 10 bermudagrass would be classified as suitable, Coastal bermudagrass would be moderately suitable, common centipedegrass would be moderately unsuitable, Tifton 292 bermudagrass would be unsuitable, and zoysiagrass would be highly unsuitable.

CHAPTER VI
GROWTH AND DEVELOPMENT OF FALL ARMYWORM ON SEQUENTIAL GRASS DIETS

Introduction

The FAW is characterized by rapid mobility and polyphagy. After overwintering in south Florida and Texas (Snow and Copeland 1969, Wood et al. 1979), the FAW moves rapidly northward in the United States where it feeds on more than 50 species of plants (Luginbill 1928). As Barfield and Stimac (1981) pointed out, most IPM strategies, especially those for highly mobile, polyphagous insects like the FAW, were designed to treat symptoms of pest problems by dealing with pest numbers in individual fields, but fail to address the real causes. To address the real causes for insect problems, an understanding of the biological and ecological mechanisms that dictate movement and feeding preference is necessary, along with a knowledge of previous management practices (Barfield 1979).

The FAW often moves from one food source to another as one host becomes limited as a food source. Thus, in outbreak years (e.g., 1977), tremendous losses to this insect might occur on several hosts (Todd and Suber 1980). In this regard, the "large-unit ecosystem heterogeneity" as emphasized by Rabb (1978) should be considered. He

suggested that an agroecosystem be conceived of as an area in which crops are grown and include those uncultivated areas which influence crops through intercommunity interchanges of organisms and materials. In such large-unit ecosystems, it is evident that variation of host plant quality may have a significant impact on insect performance, i.e., feeding, growth, reproduction, survival, and movement (Barfield and Slansky 1981). Therefore, to truly understand the population dynamics of the FAW, it is necessary to study not only its biology when feeding on a single crop, but also its biology when it moves from one host to another. These types of data are a requisite for the conceptual model for insect management as presented by Barfield and Jones (1979) or for regulating FAW populations through increased diversification of the crop agroecosystem (Altieri 1979, 1980).

However, only the effects of common centipedegrass and carpetgrass, Axonopus affinis Chase, on the FAW responses to changing host plants have been studied (Wiseman et al. 1982). The research reported herein was conducted to extend the information of FAW feeding response and development when they move from one host to another.

Materials and Methods

Four grasses (corn, Tifton 10 bermudagrass, Coastal bermudagrass, and common centipedegrass) were selected in this study. All the grasses were obtained and maintained as described above.

Initially, neonate FAW were fed en masse on each one of 4 selected grasses for 4, 6, and 8 days in 25.4 cm diam plastic dishes. After each feeding period, 30 randomly selected larvae were transferred from each host to individual plastic cups (5 cm diam, 3.5 cm high) containing wet filter paper in the bottom to provide moisture, and fed each of the other 3 hosts. As represented by C = corn, CB = Coastal bermudagrass, CP = common centipedegrass, and TB = Tifton 10 bermudagrass, the diet-switch tests with various initial feeding times are herein indicated by codes, i.e., C-4-TB = larvae switched from corn at day 4 to Tifton 10 bermudagrass, C-6-TB = larvae switched from corn at day 6 to Tifton 10 bermudagrass, C-8-TB = larvae switched from corn at day 8 to Tifton 10 bermudagrass, etc. An additional 30 larvae were transferred individually to plastic cups containing the same grass that they previously fed on for 4 days. These groups were treated as checks for comparison with the "switched" larvae.

Four separate experiments were conducted for each of the host grasses. Each experiment was arranged in a split-plot design with 30 replications. Main plots were days on selected grasses and subplots were the comparisons of FAW development on grasses to which they were transferred. The grass within each cup was replaced every day, and the tests were held in an incubator with 26.5 $\pm$ 2° C, 70 $\pm$ 5% RH and a photoperiod of LD 14:10 until all larvae pupated.

Larval weights were recorded each day after they were transferred from the grass on which they initially fed to the grass on which they would complete development. Larval growth rate of the laboratory population of FAW under constant conditions with sufficient food supply was expected to follow the exponential law (Price 1975). The correlation coefficient (r) between the logarithm of the fresh weight and age of insect was calculated. The t-test was used to test the linear relation between these two variables to determine the fit of FAW growth for the exponential growth equation for each experiment. Also, with these data, the exponential growth rate was calculated from the regression growth equation, $Y = A(B)^X$, where Y = weight in milligrams, and X = larval age in days. The relative rate of growth was calculated by multiplying the slope of the regression growth equation by 2.3026. Since the exponential growth equation (by weight) is $Y = A(B)^X$, applying logarithms to the equation yields $\log Y = \log A + (\log B)X$; and since $\ln Y = \log_e Y = (\log_{10} Y)(\log_e 10) = 2.3026 \log_{10} Y$, it follows that the constant relative rate of increase = 2.3026 x (log B) (Snedecor and Cochran 1980). Data were also recorded on larval duration, larval mortality, number of days to the first pupa, pupal weight, pupal duration, and pupal mortality. In all tests, analysis of variance of the data was calculated, and means were separated by Duncan's multiple range test.

Results and Discussion

Initial Feeding on Corn

The effects of selected grasses on the development of FAW larvae after initially feeding for 4, 6, or 8 days on corn are presented in Tables 13 and 14. Both the larval weights of C-4-TB and C-6-TB larvae were significantly ($p < 0.05$) greater than the larval weights of C-4-CB and C-6-CB, respectively. Larval weights of C-4-CB and C-6-CB were also significantly greater than larval weights of C-4-CP and C-6-CP, respectively. Compared with larvae that fed only on corn, larval weight gain was slightly faster on corn than on the other grasses. Larvae transferred to centipedegrass developed slowly, but by 8 days those larvae that survived had adapted to the new diet and showed an improved weight gain.

Developmental time was significantly greater for larvae transferred from corn to centipedegrass for all three transfer dates than for larvae transferred to either of the bermudagrasses (Table 13). Days to pupation on centipedegrass were prolonged 4-9, 22-23, and 5-6 days when transferred from corn at 4, 6, and 8 days, respectively, as compared with larval development on Tifton 10 or Coastal bermudagrass. Larvae of C-4-TB developed significantly faster than larvae of C-4-CB. However, larvae transferred at 6 and 8 days showed comparable development on these two bermudagrasses. The different time intervals that the larvae fed on corn prior to transfer to Tifton 10

Table 13
Effects of selected grasses on the development of fall armyworm larvae after initially feeding on corn for 4, 6, or 8 days[1]

Host	Initial feeding time (days) before transfer								
	4	6	8	4	6	8	4	6	8
	Larval wt. (mg) at 4 days after transfer			Days to pupation			Larval mortality (%)		
Tifton 10 bermudagrass	121.5a	217.2a	UM[2]	13.2c X	13.5b X	12.8b X	6.7	0.0	0.0
Coastal bermudagrass	41.6b	162.9b	UM	18.6b X	12.9b Y	13.0b Y	16.0	10.0	3.3
Common centipedegrass	8.5c	25.4c	233.7	22.0a Y	35.2a X	18.4a Z	93.3	80.0	28.0
Corn (Check)	183.6			12.1			0.0		

[1]Means within a column followed by the same lowercase letter and means within a horizontal line followed by the same capital letter are not significantly different at $p=0.05$, by Duncan's multiple range test.

[2]Unmeasurable because more than half of tested larvae pupated.

did not affect their developmental rate. However, C-4-CB larvae required significantly longer to pupate than C-6-CB and C-8-CB larvae. Developmental rates for larvae transferred to centipedegrass at 4, 6, and 8 days were variable; C-8-CP larvae needed significantly less time to pupate than both C-4-CP and C-6-CP larvae, and C-4-CP larvae required significantly less time to pupate than C-6-CP larvae. Apparently larvae that fed for 8 days on corn prior to transfer to the resistant centipedegrass were more able to utilize centipedegrass as a food source due to their advanced developmental stage, and larvae transferred at 4 days were better able to adapt to the new food source than were larvae transferred at 6 days.

Larval mortality (Table 13) was negligible when transferred from corn to Tifton 10, moderate when transferred to Coastal, and high when transferred to centipedegrass. A trend for increased survival with an increase in length of time that larvae had fed on corn prior to transfer to Coastal or centipedegrass was evident.

Female pupal duration was affected only for the C-4-CP larvae (Table 14). Larvae transferred to centipedegrass required significantly ($p < 0.05$) more time to complete pupal development than larvae transferred to either of the bermudagrasses. Similarly, female pupal duration was significantly longer for pupae from C-4-CB larvae than for pupae from C-4-TB larvae. Also, female pupae from C-4-CP larvae required significantly longer time to complete development than female pupae from C-6-CP and C-8-CP larvae.

Table 14
Effects of larval transfer to selected grasses after initial feeding on corn for 4, 6, or 8 days on fall armyworm pupae[1]

Host	Initial Feeding Time (Days) Before Transfer														
	Female Pupal Duration (Days)			Male Pupal Duration (Days)			Female Pupal Weight (mg)			Male Pupal Weight (mg)			Pupal Mortality (%)		
	4	6	8	4	6	8	4	6	8	4	6	8	4	6	8
Tifton 10 bermudagrass	7.2[c] X	7.7[a] X	7.7[a] X	7.8[b] X	8.3[b] X	7.8[b] X	116.8[a] Z	129.1[a] Y	139.3[a] X	125.0[a] Y	123.7[a] Y	144.6[a] X	0	3.3	0
Coastal bermudagrass	7.8[b] X	8.1[a] X	7.8[a] X	8.5[a] X	8.8[a] X	8.2[ab] X	112.0[a] Y	118.5[a] Y	135.5[a] X	114.2[a] Z	121.2[a] Y	141.2[a] X	7.1	14.8	7.1
Common centipedegrass	9.0[a] X	7.6[a] Y	8.6[a] Y	-	8.0[b] Y	9.3[a] X	131.1[a] X	89.8[b] Y	95.0[b] Y	-	102.9[b] X	93.4[b] X	0	0	27.8
Corn (Check)	7.5			8.3			141.5			156.8			10		

[1]Means within a column followed by the same lowercase letter, and means within a horizontal line followed by the same capital letter, are not significantly different at p = 0.05, by Duncan's multiple range test.

The effect of day of transfer on male pupal duration was more variable. None of the males that were transferred to centipedegrass at 4 days survived to pupate. Male pupae from C-4-CB larvae required significantly longer to complete pupal development than male pupae from C-4-TB larvae. Also, duration of male pupae from C-6-CB larvae was significantly longer than that from C-6-TB and C-6-CP larvae. Transfer at 8 days produced conflicting results in that duration for male pupae from C-8-CP was significantly longer than pupae from C-8-TB; and male pupae from C-8-CB larvae produced intermediate results. Pupal development as influenced by initial feeding time was only significant for larvae that fed on centipedegrass; larvae of C-8-CP produced male pupae that required significantly longer to complete devlopment than did larvae of C-6-CP.

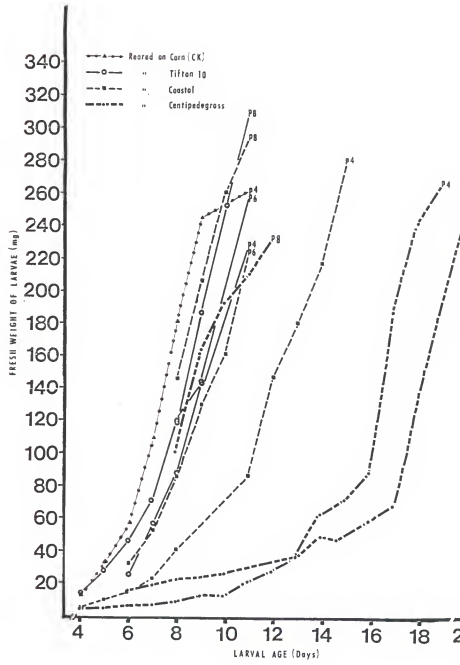
Both male and female pupal weight were significantly lower when larvae were moved to centipedegrass at 6 and 8 days, than when larvae were moved to Tifton 10 or Coastal bermudagrass (Table 14). Interestingly, however, transfer of larvae to centipedegrass at 4 days did not significantly affect female pupal weight as it did at 6 and 8 days. Only 6.7% of the C-4-CP larvae survived to pupation while 72% of the C-8-CP larvae survived to pupation (Table 13). Apparently, the small percentage of larvae that survived when transferred to centipedegrass at 4 days were able to adapt to the new host and attain a pupal weight comparable with pupal weights from the other hosts. Older larvae, i.e.,

those transferred at 6 and 8 days, did adapt to centipedegrass as a new host but produced smaller pupae. In the case where larvae were transferred at 8 days, this ability to adapt to the new centipede host and the reduced pupal weight resulted in 27.8% pupal mortality, a value considerably higher than for the other treatments.

With the exception of centipedegrass, the data in Table 14 on pupal weights also showed that the longer that larvae fed on corn prior to transfer, the greater the pupal weights. The majority of the larvae died during the larval stage when transferred to centipedegrass, especially larvae transferred at 4 and 6 days. Thus, the antibiosis effects of the resistant centipedegrass to FAW transferred at 6 and 8 days extended into the pupal stage.

Figure 5 presents the daily weight gain of FAW larvae from the day they were transferred from corn to the day of first pupation. Larvae from most treatments gained weight rapidly and pupated by 11-12 days of age. However, larval development was prolonged in three treatments. The FAW larvae of C-4-CP and C-6-CP required an extended period of time to complete development. This extended development was due to antibiosis of centipedegrass to the FAW, especially for those larvae that fed on centipede for the longer period of time. The C-4-CB larvae showed an intermediate rate of weight gain. It can be concluded that larvae transferred at 4 days from corn to Coastal bermudagrass did not readily adapt to the new host.

Figure 5. Fresh weight gain for fall armyworm larvae on selected grasses from the time that they were transferred from corn to first pupation (P). The numbers 4, 6, or 8 indicate the number of days that the insects initially fed on corn.


Reared on Corn (CK)
" Tifton 10
" Coastal
" Centipedegrass
FRESH WEIGHT OF LARVAE (mg)
LARVAL AGE (Days)
340
320
300
280
260
240
220
200
180
160
140
120
100
80
60
40
20
4
6
8
10
12
14
16
18
28
P8
P8
P4
P6
P4
P6
P8
P4
P4
P6

Initial Feeding on Tifton 10 Bermudagrass

The effects of selected grasses on the development of FAW larvae after initially feeding for 4, 6, and 8 days on Tifton 10 bermudagrass are presented in Tables 15 and 16. The FAW larval weight gain was significantly ($p < 0.05$) faster after transfer to corn than to Coastal or centipedegrass for all 3 transfer periods. Similarly, larval weight gain was significantly faster on Coastal than on centipedegrass for all 3 transfer periods. Thus, for larval weight gain, corn was the best host for larvae that had previously fed on Tifton 10 bermudagrass.

Mean larval developmental time was delayed 2-4 days when larvae were transferred to Coastal bermudagrass and 11-13 days when larvae were transferred to centipedegrass compared with larvae transferred to corn. Larval duration was significantly reduced when larvae fed on corn as compared with Coastal or centipedegrass, and significantly reduced when larvae fed on Coastal as compared with centipedegrass. Larvae of TB-6-C completed larval development significantly faster than larvae of TB-4-C or TB-8-C. Larvae of TB-8-C also required significantly less time to complete larval development than did larvae of TB-4-C. The FAW larvae transferred to Coastal bermudagrass showed a significant trend for a decrease in days to pupation with each increase in time that they had previously fed on Tifton 10 bermudagrass. All of the TB-4-CP larvae and 40% of the TB-4-CB larvae died before completing larval development.

Table 15
Effects of selected grasses on the development of fall armyworm larvae after initially feeding on Tifton 10 bermudagrass for 4, 6, or 8 days[1]

	Initial feeding time (days) before transfer								
	4	6	8	4	6	8	4	6	8
Host	Larval wt. (mg) at 4 days after transfer			Days to pupation			Larval mortality (%)		
Corn	87.3a	245.8a	330.7a	14.2b X	12.6c Z	13.5b Y	3.6	0.0	0.0
Coastal bermudagrass	14.6b	96.0b	157.7b	17.4a X	16.3b Y	15.0b Z	40.0	6.7	0.0
Common centipedegrass	3.8c	52.5c	83.2c	-	25.7a X	24.9a Y	100.0	30.0	0.0
Tifton 10 bermudagrass (Check)	26.5			17.5			3.3		

[1]Means within a column followed by the same lowercase letter and means within a horizontal line followed by the same capital letter are not significantly different at $p=0.05$, by Duncan's multiple range test.

Both male and female pupae completed development faster when FAW larvae were fed corn as compared with larvae that were fed Coastal bermudagrass or centipedegrass, with the exception of larvae transferred at 4 days that produced female pupae (Table 16). In general, pupae originating from larvae that fed on Coastal or centipedegrass required comparable times to complete development. The only exception was that female pupae from the TB-8-CP larvae required significantly ($p < 0.05$) more time to complete development than their counterparts from TB-8-CB larvae. Thus, FAW larvae transferred to corn produced pupae that generally developed more rapidly than pupae originating from larvae that fed on the other grass hosts.

There was a trend for a shorter pupal duration for larvae that fed for the longest period prior to transfer to corn. This trend was evident for both male and female pupae from corn and for female pupae from Coastal bermudagrass.

Pupal weights for FAW fed as larvae on the various grasses tended to parallel the trend for pupal duration; the treatments with the largest pupae tended to complete pupal development faster. With the exception of larvae transferred to corn and Coastal bermudagrass at 4 days, both male and female pupae from corn were significantly heavier than pupae from Coastal or centipedegrass. A comparison of pupae from the Coastal treatments with pupae from the centipedegrass treatments showedmixed results in that pupae from TB-6-CB larvae were significantly heavier

Table 16
Effects of larval transfer to selected grasses after initial feeding on Tifton 10 bermudagrass for 4, 6, or 8 days on fall armyworm pupae[1]

Host	Initial Feeding Time (Days) Before Transfer														
	4	6	8	4	6	8	4	6	8	4	6	8	4	6	8
	Female Pupal Duration (Days)			Male Pupal Duration (Days)			Female Pupal Weight (mg)			Male Pupal Weight (mg)			Pupal Mortality (%)		
Corn	7.6^{a} X	6.6^{b} Y	6.9^{c} Y	8.1^{b} X	7.4^{b} Y	7.4^{b} Y	156.4^{a} X	160.7^{a} X	154.3^{a} X	155.5^{a} X	168.4^{a} X	161.8^{a} X	3.7	0	0
Coastal bermudagrass	8.2^{a} X	8.3^{a} X	7.8^{b} Y	9.0^{a} X	8.7^{a} X	8.5^{a} X	151.5^{a} X	94.9^{b} Y	95.6^{b} Y	164.3^{a} X	113.0^{b} Y	93.7^{b} Z	5.6	0	10
Common centipedegrass	-	8.5^{a} X	8.6^{a} X	-	8.9^{a} X	8.9^{a} X	-	89.2^{c} X	82.5^{b} X	-	95.4^{c} X	92.2^{b} X	-	4.8	0
Tifton 10 bermudagrass (Check)	7.9			8.7			126.3			126.9			6.9		

[1]Means within a column followed by the same lowercase letter, and means within a horizontal line followed by the same capital letter, are not significantly different at p = 0.05, by Duncan's multiple range test.

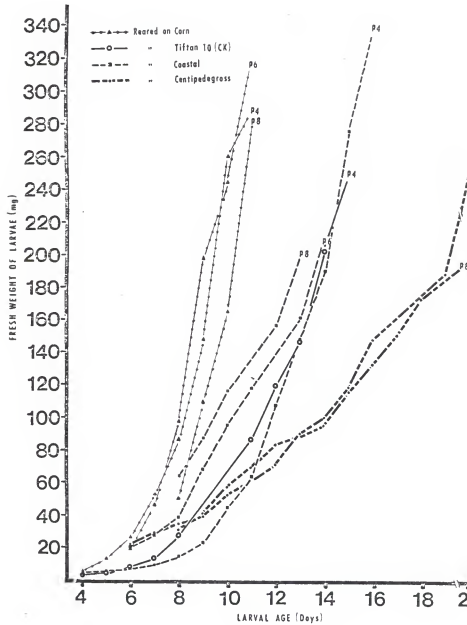
than pupae from TB-6-CP larvae, but pupal weights from larvae transferred at 8 days were comparable for the two treatments. Pupal weights from larvae that fed on corn were comparable for all three transfer periods. However, pupae from larvae that fed on Coastal bermudagrass tended to be larger, the longer the larvae fed on Coastal. Pupal mortality was negligible among all of the treatments and no trends were evident.

Figure 6 presents the average daily weight gain for larvae after their transfer from Tifton 10 bermudagrass to the day of first pupation. It is readily evident from these data that FAW development was more rapid on corn than on Coastal or centipedegrass. Larval weight gain and days to pupation were comparable on Coastal and Tifton 10 (Check) bermudagrass, but larvae on either of these two varieties developed considerably faster than larvae transferred to centipedegrass.

Initial Feed on Coastal Bermudagrass

The effects of selected grasses on the development of FAW larvae after initially feeding on Coastal for 4, 6, or 8 days are presented in Tables 17 and 18. Larval weight gain and duration after transfer to corn at 4 or 6 days was significantly ($p < 0.05$) greater and faster than for larvae transferred to Tifton 10 bermudagrass or centipedegrass (Table 17). However, larvae of CB-8-TB gained weight significantly faster than larvae of CB-8-C. These results

Figure 6. Fresh weight gain for fall armyworm larvae on selected grasses from the time that they were transferred from Tifton 10 bermuda-grass to first pupation (P). The numbers 4, 6, or 8 indicate the number of days that the insects initially fed on Tifton 10 bermudagrass.


Reared on Corn
Tifton 10 (CK)
Coastal
Centipedegrass
FRESH WEIGHT OF LARVAE (mg)
LARVAL AGE (Days)
P4
P6
P8

suggest that 6-day-old larvae were better able to adapt to corn as a host after initially feeding on Coastal, but the 8-day-old larvae were better able to adapt to Tifton 10, a close relative to Coastal bermudagrass. This hypothesis is further supported by comparisons within an individual host after transfer from Coastal bermudagrass. For example, larvae of CB-4-C and CB-6-C developed significantly faster than larvae of CB-8-C. The converse was true for larvae transferred to Tifton 10; the longer FAW larvae fed on Coastal prior to transfer to Tifton 10, the shorter the larval duration. Larvae transferred to centipedegrass also showed reduced larval duration with an increase in time on Coastal bermudagrass prior to transfer, but this trend was only significant between the 4- and 8-day transfer.

As in previous experiments, FAW larval mortality was considerably greater on centipedegrass, especially at the 4-day transfer, than mortality on the other hosts. Mortality declined on centipedegrass with each increase of time on Coastal prior to transfer. Mortality on Tifton 10 was fairly high for the initial transfer, but declined with subsequent transfer. The FAW larvae readily adapted to corn, and larval mortality was quite low on all three transfer dates.

The FAW pupal duration was not affected by either host or previous feeding time prior to transfer (Table 18). However, both previous feeding time and host influenced pupal weight. Larvae transferred to corn at day 4 or 8 produced

Table 17
Effects of selected grasses on the development of fall armyworm larvae after initially feeding on Coastal bermudagrass for 4, 6, or 8 days[1]

	Initial feeding time (days) before transfer								
	4	6	8	4	6	8	4	6	8
Host	Larval wt. (mg) at 4 days after transfer			Days to pupation			Larval mortality (%)		
Corn	51.6a	164.4a	215.0b	13.9c Y	13.7c Y	15.6b X	6.7	3.3	0.0
Tifton 10 bermudagrass	12.7b	60.7b	331.0a	20.9b X	15.6c Y	13.6c Z	20.0	3.3	12.0
Common centipedegrass	13.8b	46.1c	63.4c	24.7a X	23.1a XY	22.8a Y	50.0	13.3	8.0
Coastal bermudagrass (Check)	72.1			15.0			6.7		

[1]Means within a column followed by the same lowercase letter and means within a horizontal line followed by the same capital letter are not significantly different at $p=0.05$, by Duncan's multiple range test.

Table 18
Effects of larval transfer to selected grasses after initial feeding on Coastal bermudagrass for 4, 6, or 8 days on fall armyworm pupae[1]

Host	Initial Feeding Time (Days) Before Transfer														
	Female Pupal Duration (Days)			Male Pupal Duration (Days)			Female Pupal Weight (mg)			Male Pupal Weight (mg)			Pupal Mortality (%)		
	4	6	8	4	6	8	4	6	8	4	6	8	4	6	8
Corn	8.1[a] X	8.3[a] X	8.3[a] X	8.9[a] X	9.1[a] X	8.9[a] X	174.6[a] Y	172.8[a] Y	222.7[a] X	177.4[a] Y	176.1[a] Y	230.2[a] X	8.8	10.3	0
Tifton 10 bermudagrass	8.0[a] X	7.9[a] X	8.3[a] X	8.4[a] X	8.5[a] X	9.0[a] X	129.1[b] Y	164.2[a] X	169.4[b] X	132.4[b] Y	183.7[a] X	168.9[b] X	10.0	31.0	0
Common centipedegrass	8.0[a] X	8.1[a] X	8.2[a] X	8.8[a] X	9.1[a] X	8.8[a] X	95.9[c] X	85.4[b] X	86.6[c] X	101.8[c] X	97.7[b] X	101.8[c] X	0	3.8	8.7
Coastal bermudagrass (check)	7.7			8.4			135.3			137.0			7.1		

[1] Means within a column followed by the same lowercase letter, and means within a horizontal line followed by the same capital letter, are not significantly different at p = 0.5, by Duncan's multiple range test.

significantly ($p < 0.05$) heavier pupae, both male and female, than did larvae transferred to Tifton 10 or centipedegrass. Larvae transferred to Tifton 10 at all 3 ages produced significantly heavier male and female pupae than did larvae transferred to centipedegrass. Similarly, larvae of CB-8-C produced significantly heavier pupae than did larvae of CB-4-C and CB-6-C. This effect was also noted for Tifton 10 in that larvae of CB-6-TB or CB-8-TB produced significantly heavier pupae than did larvae of CB-4-TB.

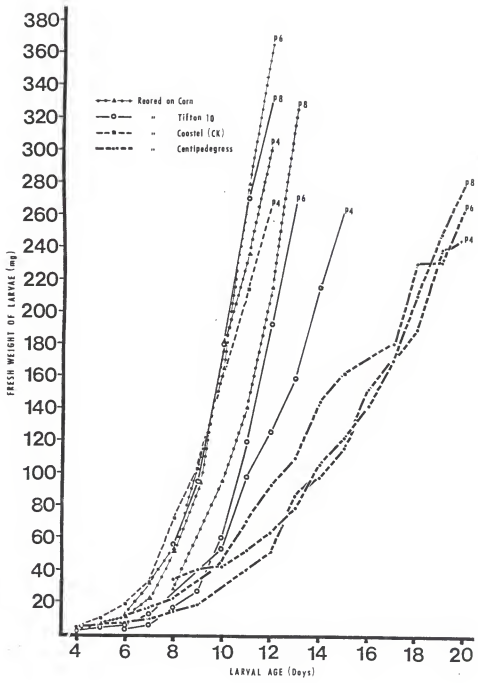
Mortality was greatest for pupae from CB-6-TB larvae (31%). Mortalities among the other treatments were fairly consistent and ranged from 0 to 10.3%.

Figure 7 presents the average daily weight gain for larvae fed the different hosts from the day of transfer from Coastal bermudagrass to first pupation. Larvae of CB-4-C and CB-6-C showed a more rapid weight gain than did larvae of CB-8-C. The opposite trend was evident for larvae transferred to Tifton 10; CB-8-TB larvae gained weight more rapidly than CB-6-TB, and CB-6-TB larvae gained weight more rapidly than CB-4-TB larvae. As in previous tests, larvae transferred to common centipedegrass showed a considerably slower weight gain than did larvae in the other treatments.

Initial Feeding on Common Centipedegrass

The effects of the selected grasses on the development of the FAW after initially feeding on common centipedegrass, a resistant host to the FAW, are presented in Tables 19 and 20.

Figure 7. Fresh weight gain for fall armyworm larvae on selected grasses from the time that they were transferred from Coastal bermudagrass to first pupation (P). The numbers 4, 6, or 8 indicate the number of days that the insects initially fed on Coastal bermudagrass.


FRESH WEIGHT OF LARVAE (mg)
LARVAL AGE (Days)
Reared on Corn
" Tifton 10
" Coastal (CK)
" Centipedegrass
P4
P6
P8

The time that FAW larvae fed on centipedegrass prior to transfer drastically affected their development when transferred to more preferred or suitable hosts (Table 19). All larvae that remained on centipedegrass, i.e., the check, throughout their development died as larvae, illustrating the high level of resistance in this grass. Weight gain was significantly ($p < 0.05$) greater for CP-4-C and CP-4-TB larvae than for CP-4-CB larvae. The same trend occurred for larval transfer at 6 days. However, CP-8-C larvae produced significantly greater weight gain than did either CP-8-TB or CP-8-CB larvae, and CP-8-CB larvae had significantly greater weight gain than CP-8-TB larvae. Larval duration was similarly affected. Larvae of CP-4-C developed significantly faster than did larvae of CP-4-TB or CP-4-CB. At 6 days, development was significantly slower on both corn and Tifton 10 than on Coastal bermudagrass. This trend was similar for CP-8-TB larvae which developed significantly slower than larvae on corn or Coastal bermudagrass.

Comparisons within a host for the three transfer times showed that for both corn and Coastal, development was faster when larvae were transferred at 8 days. Conversely, the slowest development for both corn and Tifton 10 occurred when larvae were transferred at 6 days. These results can probably be explained by the selective pressure that centipedegrass placed on the FAW larvae. By 8 days, centipedegrass had probably selected out all of the "inferior" larvae

Table 19
Effects of selected grasses on the development of fall armyworm larvae after initially feeding on common centipedegrass for 4, 6, or 8 days[1]

	Initial feeding time (days) before transfer								
	4	6	8	4	6	8	4	6	8
Host	Larval wt. (mg) at 4 days after transfer			Days to pupation			Larval mortality (%)		
Corn	28.0a	28.9a	256.0a	17.2a Y	21.1a X	14.8b Z	13.3	25.0	4.0
Tifton 10 bermudagrass	23.7a	38.4a	68.8c	19.3a Y	21.8a X	19.7a Y	16.7	39.3	0.0
Coastal bermudagrass	4.0b	13.1b	164.5b	18.9a X	18.8b X	15.4b Y	36.7	13.3	0.0
Common centipedegrass (Check)	-			-			100.0		

[1]Means within a column followed by the same lowercase letter and means within a horizontal line followed by the same capital letter are not significantly different at $p=0.05$, by Duncan's multiple range test.

so that only the most hardy or "superior" larvae remained. Thus, these "superior" larvae developed more rapidly once transferred to a suitable host. On the other hand, the selective pressure of centipedegrass had not completely eliminated the "inferior" individuals at 4 or 6 days, and development was slower once they were transferred to more suitable hosts. In the case of corn and Tifton 10, development was slowed when larvae were transferred at 6 days. These results were probably caused by incomplete selection for "superior" individuals by the sixth day, and a considerably weakened condition for the "inferior" individuals after having fed on centipedegrass for 6 days. This hypothesis is further supported by the mortality data in Table 19. Mortality in all 3 hosts was quite substantial for the 4-day transfer, but was considerably greater for larvae transferred to Coastal in comparison with larvae transferred to corn or Tifton 10. At 6 days, mortality of larvae transferred to corn and Tifton 10 increased substantially over their counterparts transferred at the 4 days. Mortality for larvae transferred at 8 days was negligible and considerably lower than for the previous transfer times, probably as a result of the selective pressure of centipedegrass noted above.

Data pertaining to FAW pupae are presented in Table 20. Duration of both male and female pupae from CP-4-C or CP-4-CB larvae was significantly ($p < 0.05$) shorter than pupal duration for CP-4-TB larvae. For larvae transferred

Table 20
Effects of larval transfer to selected grasses after initial feeding on common centipedegrass for 4, 6, or 8 days on fall armyworm pupae[1]

Host	Initial Feeding Time (Days) Before Transfer														
	4	6	8	4	6	8	4	6	8	4	6	8	4	6	8
	Female Pupal Duration (Days)			Male Pupal Duration (Days)			Female Pupal Weight (mg)			Male Pupal Weight (mg)			Pupal Mortality (%)		
Corn	8.4[b] X	8.0[a] X	8.2[a] X	8.8[b] X	8.7[b] X	8.9[b] X	169.1[a] Y	150.9[a] Y	204.9[a] X	166.7[a] Y	157.9[a] Y	210.5[a] X	7.7	0	0
Tifton 10 bermudagrass	8.9[a] X	8.1[a] Y	8.1[a] Y	9.8[a] X	7.8[b] Y	9.2[a] X	126.7[b] X	123.4[b] X	126.8[b] X	117.6[b] X	130.5[b] X	131.2[b] X	24.0	11.8	13.3
Coastal bermudagrass	8.3[b] X	8.3[a] X	7.6[b] Y	8.8[b] X	9.0[a] X	8.6[b] X	154.0[a] X	148.6[a] X	106.5[c] Y	158.8[a] X	175.2[a] X	122.0[b] Y	0	3.8	18.2
Common centipedegrass (check)	-			-			-			-			-		

[1]Means within a column followed by the same lowercase letter, and means within a horizontal line followed by the same capital letter, are not significantly different at p = 0.05, by Duncan's multiple range test.

at 6 days, only the males showed an effect related to host; duration of male pupae was significantly longer for CP-6-CB larvae than for CP-6-C and CP-6-TB larvae. Larvae transferred at 8 days showed a similar trend for female pupae but not for male pupae. Male pupae from CP-8-TB larvae required more time to complete development than did male pupae from CP-8-C or CP-8-CB larvae. Thus, overall there were no consistent trends for pupal duration that were related to host.

Comparison of pupal duration within a host as related to age at larval transfer showed that age at transfer did not influence either male or female pupal duration when the larvae were transferred to corn. However, age at transfer did affect pupal duration, especially for females, when larvae were transferred to either Coastal or Tifton 10 bermudagrass. Female pupal duration was significantly reduced for pupae from CP-6-TB or CP-8-TB larvae compared with pupae from CP-4-TB larvae. Pupae originating from CP-8-CB larvae developed significantly faster compared with pupae from CP-4-CB or CP-6-CB larvae.

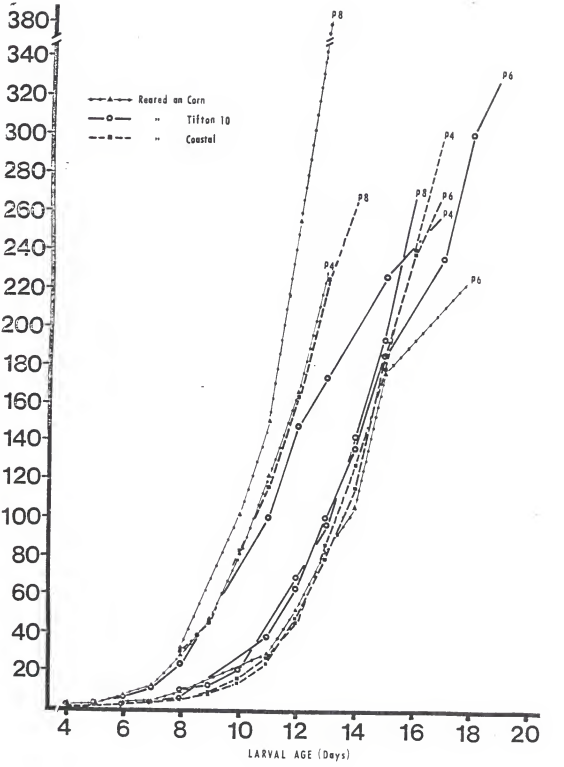
Pupal weight for these treatments are presented in Table 20. Both male and female pupae were significantly heavier for larvae transferred at 4 and 6 days to corn or Coastal than for larvae transferred to Tifton 10. At the 8-day transfer, female pupae originating from CP-8-C larvae were significantly heavier than pupae from CP-8-TB or CP-8-CB larvae, and pupae from CP-8-TB larvae were

significantly heavier than pupae from CP-8-CB larvae. Male pupae from the larvae that fed on corn were also significantly heavier than pupae from larvae that fed on either of the bermudagrasses.

Pupal mortality was highest for larvae that fed on Tifton 10, especially for those transferred at 4 days. Pupal mortality declined with increasing age at transfer for larvae that were fed corn. However, the opposite was true for pupae from Coastal bermudagrass.

Figure 8 presents the average daily weight gain for larvae fed the different hosts from the day they were transferred from centipedegrass to first pupation. The fastest weight gain and shortest larval duration were recorded for larvae of CP-8-C. Larvae of CP-4-C, CP-8-CB, or CP-4-TB showed an intermediate weight gain and, for corn and Coastal, and intermediate larval duration. The slowest weight gain and longest larval duration were recorded for larvae transferred to any of the three hosts at 6 days, to Coastal at 4 days or to Tifton 10 at 8 days. These data further support the hypothesis that the FAW-resistant centipedegrass initially weakened the larvae (i.e., 4 and 6 days prior to transfer), but by 8 days only the most hardy larvae survived. Once these hardy larvae were transferred to suitable, acceptable hosts such as corn, they developed very rapidly.

Figure 8. Fresh weight gain for fall armyworm larvae on selected grasses from the time that they were transferred from common centipedegrass to first pupation (P). The numbers 4, 6, or 8 indicate the number of days that the insects initially fed on common centipedegrass.


Reared on Corn
" Tifton 10
" Coastal
P8
P6
P4
P8
P8
P6
P4
P4
P6
380
340
320
300
280
260
240
220
200
180
160
140
120
100
80
60
40
20
4
6
8
10
12
14
16
18
20
LARVAL AGE (Days)

Exponential Growth Equation and Relative Growth Rates

The correlation coefficient (r) of all the treatments ranged from 0.884 to 1.000 and were significant at the $p = 0.05$ level (Table 21). Thus, the exponential growth equation fits insect growth for all treatments in this study.

The exponential growth equations were calculated from each growth curve presented in Figures 5, 6, 7, and 8 and were used to compare relative growth rates (RGR) of FAW larvae on the various hosts. The highest RGR values indicate the most suitable host(s) for FAW development. The RGR for FAW reared continuously on corn (0.4351 mg/day/mg) was, with only one exception (i.e., CP-6-C), lower than the growth rates for FAW that initially fed on any of the other three grasses prior to transfer to corn. Thus, corn is a suitable host, but is most effectively utilized after FAW larvae had previously fed on one of the other grasses as exemplified by higher RGR values. Two plausible explanations may explain this phenomenon. First, corn at the particular stage utilized may be deficient in some nutritional element that enhances early larval growth. This nutritional element may be found in the other grasses, and, after this nutritional requirement has been met, larvae transferred to corn develop more rapidly than if they had fed on this stage of corn during the entire larval stage. Second, corn is preferred by FAW larvae for feeding as indicated by the result of Chapter III. If larvae were

Table 21

Correlation coefficient, exponential growth equations and relative growth rates for fall armyworm larvae on selected hosts after initially feeding for 4, 6, or 8 days on corn, Tifton 10 bermudagrass, Coastal bermudagrass, or common centipedegrass

Correlation Coefficient,[1] Exponential Growth Equations,[2] and Relative Growth Rates[3]

Transfer Host	Initial Hosts and Larval Age (Days) at Transfer											
	Corn			Tifton 10 Bermudagrass			Coastal Bermudagrass			Common Centipedegrass		
	4	6	8	4	6	8	4	6	8	4	6	8
Corn	r=0.942*[4] y=1.85(1.55)^x (0.435)[5] (check)	-	-	r=0.990* y=0.78(1.77)^x (0.5710)	r=0.976* y=0.89(1.76)^x (0.5625)	r=0.993* y=0.62(1.75)^x (0.5560)	r=0.991* y=0.27(1.87)^x (0.6242)	r=0.994* y=0.61(1.74)^x (0.5519)	r=0.991* y=0.64(1.63)^x (0.4863)	r=0.982* y=0.13(1.85)^x (0.6184)	r=0.969* y=0.21(1.54)^x (0.4333)	r=0.988* y=0.64(1.44)^x (0.4967)
Tifton 10 bermudagrass	r=0.991* y=1.71(1.43)^x (0.3558)	r=0.970* y=2.32(1.56)^x (0.4439)	r=0.964* y=10.33(1.37)^x (0.3150)	r=1.000* y=0.19(1.69)^x (0.5259) (check)	-	-	r=1.000* y=0.34(1.61)^x (0.4753)	r=0.995* y=0.05(1.99)^x (0.6864)	r=0.989* y=1.51(1.59)^x (0.4628)	r=0.959* y=0.44(1.54)^x (0.4200)	r=0.964* y=0.22(1.53)^x (0.4251)	r=0.993* y=0.20(1.59)^x (0.4651)
Coastal bermudagrass	r=0.961* y=8.38(1.38)^x (0.3104)	r=0.974* y=3.72(1.47)^x (0.3820)	r=1.000* y=24.17(1.26)^x (0.2330)	r=0.995* y=0.59(1.51)^x (0.4133)	r=0.971* y=3.72(1.35)^x (0.3003)	r=0.985* y=12.41(1.24)^x (0.2148)	r=0.964* y=0.78(1.68)^x (0.5160) (check)	-	-	r=0.994* y=0.07(1.69)^x (0.5225)	r=0.987* y=0.07(1.68)^x (0.5188)	r=1.000* y=1.74(1.45)^x (0.3723)
Common centipedegrass	r=0.987* y=0.94(1.34)^x (0.2945)	r=0.992* y=2.40(1.14)^x (0.1301)	r=0.930* y=25.26(1.21)^x (0.1911)	-	r=0.994* y=10.16(1.17)^x (0.1560)	r=0.986* y=12.30(1.16)^x (0.1458)	r=0.988* y=1.66(1.31)^x (0.2712)	r=0.844* y=2.61(1.30)^x (0.2610)	r=0.997* y=7.20(1.20)^x (0.1858)	- - (check)	-	-
Reference[6]	Figure 5			Figure 6			Figure 7			Figure 8		

[1] Correlation coefficient (r) between the logarithm of larval weight and age of insect; significance (*) tested by t test at p = 0.05 level.

[2] Exponential growth equation, y = A(B)^x where y = larval weight, x = larval age by day, A and B are constants to be estimated.

[3] Relative growth rate (mg/day/mg) shown in parentheses.

[4] Correlation coefficient, exponential growth equation and relative growth rates calculated from data presented in Figures 5, 6, 7, and 8.

initially fed a nonpreferred host or a host with antibiosis, there may be a synergistic effect when the larvae are transferred to a suitable and preferred host such as corn.

The FAW larvae that were continuously fed on Tifton 10 or Coastal generally had higher RGR values than when larvae were transferred to these grasses from other hosts. Thus, FAW larvae that initially fed on thse bermudagrasses generally are able to adapt better to a new host than if they were transferred to these bermudagrasses after initially feeding on another host.

The antibiosis type of resistance found in centipedegrass is further demonstrated by the low RGR values of larvae transferred to this grass from the other hosts. The FAW larvae forced to feed on centipedegrass throughout their life died before attaining the pupal stage, and, thus, an RGR value could not be calculated. When FAW larvae were intially fed on other hosts prior to transfer to centipedegrass or larvae were initially fed on centipedegrass and then transferred to other hosts, the larvae were generally able to complete development. However, when the larvae were transferred to centipedegrass from the other hosts, the RGR value was very low and ranged from 0.1301 to 0.2945 mg/day/mg.

The high mobility and polyphagous nature of the FAW results not only in the infestation of many agricultural areas and crops, but also in a high degree of difficulty in predicting and understanding its population dynamics.

This study focused on the effects of selected host grasses on the developmental biology of the FAW when larvae were allowed to feed on one particular host for various periods of time prior to being transferred to different hosts. From the results, it is obvious that the rate of larval weight gain, duration, and mortality, and pupal weight, duration, and mortality are all dramatically influenced by the host on which FAW larvae initially establish and feed as well as the host on which they complete their development. In several instances, there were definite interactions between the initial feeding time on a host and the host on which larvae completed development that either enhanced or delayed larval and/or pupal development.

CHAPTER VII
QUANTITATIVE FOOD UTILIZATION BY FALL ARMYWORM LARVAE ON SELECTED GRASSES

Introduction

Luginbill (1928) included the records obtained by R. A. Vickery that ca. 90 cm^2 of corn and by Samuel Blum that ca. 13.8 cm^2 of crabgrass were needed per FAW to complete the immature stage. Since then, many measurements of leaf consumption of FAW on various host plants have been done, e.g., corn (Wiseman et al. 1981), peanuts (Barfield et al. 1980b, Lynch et al. 1981, Garner and Lynch 1981), other grasses and sedges (Pencoe and Martin 1981, 1982b, Lynch et al. 1983). Generally, those leaf consumption measurements were studied either for establishing economic injury levels (e.g., Martin et al. 1980) or as a parameter for evaluating host suitability and host plant resistance (e.g., Lynch et al. 1981).

The analysis of food intake, food utilization, and insect growth have been studied for various insects on various host plants (Waldbauer 1968, Slansky and Scriber 1982). Nevertheless, for polyphagous insects, most studies focused on the southern armyworm, Spodoptera eridania (Cramer). Soo Hoo and Fraenkel (1966) tested the consumption, digestion, and utilization of 18 different food

plants (13 families) by this insect. The consumption and utilization of birdsfoot trefoil (Lotus corniculatus) containing different amounts of cyanogenic glycosides by southern armyworm larvae were reported by Scriber (1978b). Scriber (1979) studied the postingestive utilization of plant biomass and nitrogen of S. eridania on selected variety of species of Leguminoseae. The effects of sequential diets and associated metabolic costs were also studied by Scriber (1981) in feeding this insect on dill (Anethum graveolens) lima beans (Phaseolus lunatus) and cabbage (Brassica oleraceae). Manuwoto and Scriber (1982) reported the consumption and utilization by S. eridania of three different corn varieties which contain different concentrations of DIMBOA [2,4-dihydroxy-7-methoxy (2H)-1,4-benzoxazin (4H) one]. Although the polyphagous FAW, similar to the southern armyworm, can accept many species of food plants from different families, published studies dealing with the rates of food intake, digestibility, and the efficiency of conversion of diets for this pest are lacking.

The present study was undertaken to (1) measure the consumption of selected grass plants by the FAW throughout its larval development, (2) analyze the digestibility, the conversion of digested food and the consumption rate of FAW feeding upon selected grasses, and (3) use the method of sequential diets to investigate the postingestive utilization of susceptible or resistant grass plants by FAW.

Materials and Methods

Six selected grasses in this study were Coastal, Tifton 10, Tifton 292 bermudagrass, common centipedegrass, zoysiagrass, and corn. Cultures of each grass were obtained and maintained by the same way as previously described. The FAW larvae were obtained from the laboratory culture at IBPMRL, Tifton, Georgia.

Leaf Consumption per Instar

The freshly excised leaves of corn, Tifton 10, and Coastal bermudagrass were weighed (A) prior to FAW larval feeding. First instars (36 for each grass) were placed individually on the weighed leaves and confined in plastic cups (5 cm diam, 3.5 cm high) which contained moist filter paper in the bottom. An additional group of 5 cups containing weighed leaves (E) and the moist filter paper were used in each instar test to check for weight changes due to leaf metabolism during each feeding period. All cups were maintained in an incubator with 26.7 $\pm$ 2° C, 70 $\pm$ 5% RH and a photoperiod of LD 14:10. Five sets of excised leaves were weighed and oven-dried at 60° C for 24 hr. to obtain the average percentage of dry weight (B).

Larvae were checked daily. At the beginning of the 2nd-instar, 18 uniformly molting larvae were used to test the leaf consumption of each subsequent instar. After each molt, the unconsumed leaf material was oven-dried to determine its dry weight (C). The dry weight of the leaves in

the five check cups were also determined (F). The average metabolic loss (D) of the tested grasses was obtained from the formula D = (E x B)-F. Food consumption (CR) of FAW on each grass was calculated from the formula CR = (A x B) - (C + D).

Analysis of variance was used to test for differences in consumption of each instar among the grasses. The treatment means were separated by using Duncan's multiple range test.

Food Consumption and Utilization on Selected Grasses

The postingestive utilization of corn, Tifton 10 and Coastal bermudagrass, as well as the artificial pinto bean diet, by individual FAW larvae were determined using a standard gravimetric technique (Waldbauer 1968). The artificial diet was used for comparison with the grasses to evaluate the difference in postingestive utilization associated with consumption of the different grasses.

About 50 neonate FAW were confined in 25 cm diam dishes and fed each selected grass. Freshly excised grass leaves were added every day until the larvae reached the penultimate stage. Other larvae were maintained on artificial diet in plastic rearing cups as described by Perkins (1979). Ten to 15 newly molted final (6th) instar FAW larvae determined by discarded head capsules from each tested diet were weighed less than 3 hr. after ecdysis. Larvae were then placed individually in plastic cups (5 cm diam, 3.5 cm

high) containing the same food they fed on previously. The cups were maintained under the constant environment described above.

Another 5 FAW larvae, which were picked up from each tested diet and samples of each test diet, were weighed wet and then dried to a constant weight (60° C, 24 hr.) to determine the dry weight percentage. This permitted the dry weight of the introduced insect and food to be calculated, respectively. After 24 hr. of feeding, the FAW larvae, the remaining food, and the feces were removed, weighed wet, and oven-dried at 60° C for 24 hr. The following parameters of larval growth and feeding efficiency were calculated (Waldbauer 1968, Scriber and Slansky 1981):

AGR: Absolute Growth Rate

= mg (dry wt.) of biomass gained / day

= ACR x ECI

RGR: Relative Growth Rate

= mg (dry wt.) of biomass gained / mg (dry wt.) of larval biomass / day

ACR: Absolute Consumption Rate

= mg (dry wt.) of food ingested / day

RCR: Relative Consumption Rate

= mg (dry wt.) of biomass ingested / mg (dry wt.) of larval biomass / day

AD: Approximate Digestibility

$$= \frac{\text{Food ingested (mg dry wt.) - feces (mg dry wt.)}}{\text{Food ingested (mg dry wt.)}} \times 100$$

ECD: Efficiency of Conversion of Digested Food

$$= \frac{\text{Biomass gained (mg dry wt.)}}{\text{Food ingested (mg dry wt.)} - \text{feces (mg dry wt.)}} \times 100$$

ECI: Efficiency of Conversion of Ingested Food

$$= \frac{\text{Biomass gained (mg dry wt.)}}{\text{Food ingested (mg dry wt.)}} \times 100$$

$$= \text{AD} \times \text{ECD}$$

Means of these rates and efficiences for larvae fed the selected grasses were subjected to ANOVA and Tukey's studentized range test (Winer 1971).

Food Consumption and Utilization on Sequential Diets

Seven different diets, i.e., pinto bean diet, corn, Coastal, Tifton 10, Tifton 292 bermudagrass, common centipedegrass and zoysiagrass, were used in this sequential diet test. The FAW larvae were first fed the suitable pinto bean diet or the susceptible grasses, corn and Tifton 10 bermudagrass. Freshly molted 6th-instar larvae were then weighed and switched individually to 7 different grasses or diet. Food consumption and utilization were estimated by the gravimetric technique described above. Calculation of the food utilization parameters, statistical analysis, and the separation of difference between means were the same as previously. Thus, in this experiment, the postingestive performance of final instar FAW on 7 selected diets were

compared after they were fed initially on the three suitable diets.

A second switching experiment involved first feeding larvae on Coastal bermudagrass or common centipedegrass and then switching them to selected grasses. The performance values from this experiment were then compared with those values obtained in the first switching experiment to evaluate the effects of initial diet on the performance of FAW larvae. Finally, a third experiment examined quantitative food utilization by FAW larvae that were switched between two grasses, the susceptible Coastal bermudagrass and the resistant common centipedegrass. In these two experiments, identical methods were used as described above for the first experiment.

Results and Discussion

Leaf Consumption per Instar

The first two instars of FAW larvae consumed significantly ($p < 0.05$) more Tifton 10 bermudagrass than corn or Coastal bermudagrass (Table 22). This was believed to be due to the high preference for Tifton 10 by neonate larvae as indicated in Chapter III. Although 3rd-instar FAW consumed slightly more corn or Tifton 10 bermudagrass than Coastal bermudagrass, these differences were not significant. The amount of Coastal consumed by 4th-instar larvae was significantly less than that of corn or Tifton 10, ca. one-third as much. The 5th- and 6th-instar FAW larvae consumed

Table 22
Fall armyworm leaf consumption by instar
on corn, Tifton 10 and Coastal bermudagrasses[1,2]

Grass	Leaf consumption (mg of dry wt.) per larvae by larval instar					Total
	1st & 2nd	3rd	4th	5th	6th	
Corn	2.7 ± 1.0b (1.0%)	10.9 ± 4.8a (4.0%)	43.3 ± 18.7a (16.0%)	67.5 ± 15.3a (25.0%)	145.9 ± 39.7a (54.0%)	270.3 (100%)
Tifton 10 bermuda-grass	5.0 ± 3.4a (2.1%)	10.3 ± 3.2a (4.4%)	40.2 ± 14.5a (17.3%)	58.7 ± 12.4b (25.2%)	118.5 ± 22.7b (50.9%)	232.7 (100%)
Coastal bermuda-grass	2.8 ± 1.0b (1.8%)	8.6 ± 2.7a (5.7%)	13.3 ± 3.2b (8.7%)	45.7 ± 7.3c (30.0%)	82.0 ± 12.6c (53.8%)	152.4 (100%)

[1]Data expressed as Mean ± 1 SD. Means within each column not followed by the same letter are significantly different at the $p=0.05$ level by Duncan's multiple range test.

[2]Data in parentheses indicate the percentage consumption by instar.

significantly more corn/larvae than both bermudagrasses, and significantly more Tifton 10 than Coastal.

Values of total leaf consumption throughout larval development on corn, Tifton 10, and Coastal bermudagrass were 270.3 mg, 232.7 mg, and 152.4 mg, respectively. The disparity in consumption among these three grasses was possibly due to the preference for corn by the FAW larvae and/or differences in postingestive food utilization efficiencies.

About 5% to 7.5% of the total leaf weight of all three grasses was consumed by the first three instars, and more than 75% of the total consumption occurred during the last two instars. These results were similar to the results of Garner and Lynch (1981) who measured the leaf consumption of FAW larvae on Florunner peanuts. Therefore, the penultimate and final instars of FAW are the most destructive stages. The monitoring and management of FAW populations in the field, then, should be conducted before these instars have been reached.

Food Consumption and Utilization on Selected Grasses

Significantly higher growth rates (both AGR and RGR) were observed for final instar larvae on pinto bean diet than on the three grasses (Table 23). The RGR of larvae on pinto bean diet was about 1.4 times greater than that on corn, 1.2 times greater than on Tifton 10, and 2.4 times greater than on Coastal bermudagrass. This high growth rate is related to the high efficiency of conversion of

ingested food into biomass (ECI) of larvae on the pinto bean diet, and not to a high larval consumption rate (Table 23). Moreover, this higher efficiency was not due to a difference in digestive efficiency (AD) but rather to a significant difference in converting digested food into biomass (ECD). Slansky and Scriber (1982) summarized the performance values for the immature stage of various arthropods in different feeding guilds. Comparing FAW larval performance on the pinto bean diet with the average value for Lepidoptera larvae fed on artificial diets (0.07 mg/mg/day) in Slansky and Scriber (1982), indicated, surprisingly, an RGR value for FAW about 13-fold greater. Both higher RCR and ECD values contributed to this high RGR of the FAW larvae. Thus, the suitability of pinto bean diet to FAW was reflected by the low metabolic costs of processing it and by the high consumption rate of the larvae.

Among the grasses, a significantly lower growth rate was observed for larvae on Coastal bermudagrass (Table 23). Because there were no statistically significant differences in AD or ECD for larvae feeding on corn, Tifton 10, and Coastal bermudagrass, the lower growth is obviously due to the significantly lower consumption of larvae on Coastal bermudagrass. This low consumption was associated with a significantly lower water content in the leaves of Coastal bermudagrass. Although the leaf water content of corn was significantly higher than that of Tifton 10, there were no statistical differences between larval performances on these two grasses (except in ACR).

Table 23
Growth rates, consumption rates, and efficiencies of 6th-instar fall armyworm on selected grasses and pinto bean diet[1]

Diets	Diet water content (%)	Growth rates		Consumption rates		Efficiency			No. of larvae
		AGR (mg/day)	RGR (mg/mg/day)	ACR (mg/day)	RCR (mg/mg/day)	AD (%)	ECD (%)	ECI (%)	(n)
Pinto bean diet (CK)	75.4b (0.2)	51.4a (1.6)	0.9a (0.02)	164.5a (4.6)	2.8b (0.06)	33.4a (2.9)	85.5a (4.3)	31.3a (0.9)	12
Corn	83.0a (0.5)	27.6b (1.3)	0.6b (0.03)	161.6a (0.6)	3.8a (0.3)	34.3a (3.0)	57.0b (7.4)	17.5b (1.1)	12
Tifton 10 bermudagrass	72.1c (0.2)	24.5b (0.7)	0.7b (0.01)	130.9b (4.5)	4.0a (0.1)	33.6a (1.9)	59.2b (4.2)	18.9b (0.5)	15
Coastal bermudagrass	68.9d (0.4)	8.1c (1.1)	0.4c (0.05)	53.1c (2.8)	2.4b (0.1)	37.0a (4.7)	47.8b (7.6)	15.3b (1.8)	11
HSD[2]	1.3*	4.5*	0.1*	22.5*	0.6*	11.8	12.3*	4.1*	

[1]All data were calculated on a dry-weight basis and presented as Mean ± (1 SE).

[2]HSD. Honestly significant difference between means ($p=0.05$) (*), using Tukey's studentized range test for unequal sample sizes.

Comparing FAW larval performances on corn, Tifton 10, and Coastal bermudagrass (Table 23) with the average performance values of grass-chewing Lepidoptera (Slansky and Scriber 1982), FAW larvae had a higher RCR, ranging from 1.2- to 2.0-fold greater than the average value. The high RCR was presumably the major reason for the higher growth rates of FAW larvae on these grasses. Overall conversion efficiency (ECI) values for FAW (15.4-18.9%) were slightly lower than the average ECI (19%) for grass-chewing Lepidoptera larvae. Thus, it is apparent that FAW is one of the most destructive pests on its preferred grasses, not only because of high mobility and polyphagy (Barfield et al. 1980a), but also because of its high consumption rate.

Food Consumption and Utilization on Sequential Diets

Most larvae failed to complete their development when continuously fed on some resistant grasses such as Tifton 292 bermudagrass and zoysiagrass (Chapter V). Thus, the suitable pinto bean diet was fed to larvae prior to their transfer to the various grasses. Growth performance of final instars on the grasses is presented in Table 24.

Larvae continuously fed on pinto bean diet had a significantly higher RGR than larvae transferred to the various grasses. This high growth rate was due to a significantly higher ECD but not to consumption rate differences, as found in the previous experiment. Among the grass diets, the RGR was highest on corn, intermediate on Tifton 10 or

Coastal bermudagrass, and significantly lower on common centipedegrass, Tifton 292 bermudagrass, or zoysiagrass. Both differences in ECI and RCR were responsible for the variation in RGR (0.02 to 0.6 mg/mg/day) of larvae under these sequential treatments.

Corn leaves had a significantly higher water content (86.0%) than the other grasses; the significantly higher RCR of larvae on corn, combined with the high ECI, resulted in the highest RGR on corn among all the grass diets. The RGR of larvae on Tifton 10 and Coastal bermudagrass were only 66.7% and 50.0%, respectively, of the RGR of larvae on corn. The RCR values for larvae on these two bermudagrasses were statistically lower than that on corn. However, both the higher RCR and ECI values contributed to the higher RGR of larvae on these two bermudagrasses than on other three unsuitable grasses.

Scriber (1979) mentioned that the variation in nutritional quality played an important role in determining larval growth rate and utilization efficiencies of "adapted" herbivores. Meanwhile, Feeny (1976) indicated that the adaptations associated with herbivores feeding on "apparent" plants may be largely a result of the limitations imposed by the quantitative types of defenses such as low leaf water content. The differences among RCR for FAW larvae feeding on corn, Tifton 10 or Coastal bermudagrass (Tables 23, 24), thus, is presumably due to the different nutritional quality (including leaf water content) of these three grasses.

Table 24
Growth rates, consumption rates, and efficiencies of 6th-instar fall armyworm on selected grasses after initially fed on pinto bean diet[1]

Diets	Diet water content (%)	Growth rates		Consumption rates		Efficiency			No. of larvae
		AGR (mg/day)	RGR (mg/mg/day)	ACR (mg/day)	RCR (mg/mg/day)	AD (%)	ECD (%)	ECI (%)	(n)
Pinto bean diet (CK)	75.4bc (0.2)	51.4a (1.6)	0.9a (0.02)	164.5a (4.6)	2.8b (0.1)	33.4a (2.9)	85.5a (4.3)	31.3a (0.9)	12
Corn	86.9a (1.7)	22.3b (1.4)	0.6b (0.02)	138.5ab (13.6)	3.5a (0.3)	41.3a (4.5)	49.2b (8.5)	17.2b (1.5)	12
Tifton 10 bermudagrass	74.0c (0.2)	18.4b (2.4)	0.4c (0.08)	112.5b (8.8)	2.3bc (0.2)	37.1a (1.5)	45.4b (6.5)	16.8b (2.6)	12
Coastal bermudagrass	67.3d (0.4)	8.4c (1.4)	0.3c (0.01)	69.9c (4.4)	1.8cd (0.1)	27.4a (2.9)	48.1b (9.4)	12.5bc (2.3)	15
Common centipedegrass	77.3b (0.2)	2.7d (0.8)	0.1d (0.02)	45.8cd (3.7)	1.3de (0.1)	41.1a (2.5)	16.1c (6.6)	5.7c (1.8)	12
Tifton 292 bermudagrass	66.2d (0.3)	0.6d (0.4)	0.02d (0.01)	30.5d (3.2)	0.7e (0.1)	28.9a (4.0)	2.9c (0.01)	4.3c (3.3)	15
Zoysiagrass	65.6d (0.3)	3.7cd (0.8)	0.1d (0.02)	42.3d (2.5)	1.1e (0.1)	27.6a (3.9)	30.5bc (8.7)	8.5bc (1.8)	15
HSD[2]	2.7*	5.7*	0.2*	27.5*	0.6*	14.6	28.6*	9.7*	

[1]All data were calculated on a dry-weight basis and presented as Mean ± (1 SE).

[2]HSD. Honestly significant difference between means ($p=0.05$) (*), using Tukey's studentized range test for unequal sample sizes.

For larvae transferred to common centipedegrass, Tifton 292 bermudagrass, or zoysiagrass, growth was significantly slower on these resistant grasses than on either corn or the two bermudagrasses (Table 24). This growth suppression was not mediated via a reduction in AD, but instead via greater metabolic expenditures (as reflected by a reduced ECD) and a reduction in the consumption rate. Because ECD may reflect metabolic costs associated with detoxification of allelochemicals, as well as energy "waste" associated with production of metabolic water (Fraenkel and Blewett 1944, Scriber 1978a), the low ECD values of larvae on these resistant grasses indicate that potential allelochemical(s) may be present. The reduction of RGR of larvae on the resistant Tifton 292 bermudagrass and zoysiagrass might also be the result of a high fiber content which reduced AD (although not significantly) for larvae feeding on these plants.

Table 25 presents the performance of larvae on 7 selected diets after they initially fed on corn. The highest growth rate occurred on pinto bean diet, associated with a high RCR (3.9 mg/mg/day) as well as a significantly higher ECI (25.4%). Performance of larvae on Tifton 10 bermudagrass, Coastal bermudagrass and common centipedegrass was not significantly different from that on corn with the exception of the low RCR for larvae on Coastal bermudagrass. The significantly lower growth was found after larvae were switched to Tifton 292 bermudagrass and zoysiagrass (0.2

Table 25
Growth rates, consumption rates, and efficiencies of 6th-instar fall armyworm on selected grasses and pinto bean diet after initially fed on corn[1]

Diets	Diet water content (%)	Growth rates		Consumption rates		Efficiency			No. of larvae
		AGR (mg/day)	RGR (mg/mg/day)	ACR (mg/day)	RCR (mg/mg/day)	AD (%)	ECD (%)	ECI (%)	(n)
Pinto bean diet	73.3c (0.3)	37.4a (1.3)	1.0a (0.1)	150.6ab (8.1)	3.9a (0.3)	49.1a (1.9)	53.0ab (3.4)	25.4a (1.0)	14
Corn	83.0a (0.5)	27.6b (1.3)	0.6b (0.03)	161.6a (9.6)	3.8ab (0.3)	34.3abc (3.0)	57.0a (7.4)	17.6bc (1.1)	12
Tifton 10 bermudagrass	76.2b (1.1)	25.8b (2.5)	0.7b (0.1)	120.9bc (9.6)	3.1bc (0.1)	40.6ab (1.6)	52.8ab (2.7)	21.5ab (1.5)	11
Coastal bermudagrass	66.7d (0.3)	14.1c (0.9)	0.5b (0.03)	69.4de (3.4)	2.5c (0.1)	41.3ab (1.6)	50.3ab (2.7)	20.3ab (0.6)	15
Common centipedegrass	78.8bc (0.4)	15.9c (1.0)	0.5b (0.02)	95.8cd (7.2)	3.1bc (0.1)	30.9bc (1.3)	57.3a (5.9)	17.0bc (1.1)	11
Tifton 292 bermudagrass	66.0d (0.6)	8.0d (1.8)	0.2c (0.04)	52.6ef (8.7)	1.5d (0.2)	28.8b (6.0)	47.9ab (9.2)	14.0cd (1.3)	9
Zoysiagrass	62.5e (0.4)	3.0d (0.6)	0.1c (0.03)	27.7f (3.1)	1.4d (0.2)	25.1c (6.0)	29.3b (8.8)	11.0d (2.1)	15
HSD[2]	2.5*	5.9*	0.2*	30.6*	0.8*	15.7*	26.7*	6.0*	

[1]All data were calculated on a dry-weight basis and presented as Mean ± (1 SE).
[2]HSD. Honestly significant difference between means ($p=0.05$) (*), using Tukey's studentized range test for unequal sample sizes.

and 0.1 mg/mg/day, respectively). Both the lower ECI and RCR were responsible for the depression of RGR on these two grasses.

Growth performances on various grasses by larvae after previously fed on Tifton 10 bermudagrass, the most preferred grass of FAW, is presented in Table 26. The RGR of larvae transferred to pinto bean diet or corn was significantly higher than larvae continuously fed on Tifton 10. The RCR values (3.7 to 4.0 mg/mg/day) were not statistically different among these three diets. Thus, the significantly higher ECI values of larvae on pinto bean diet and corn compared to larvae on Tifton 10 (1.5 times and 1.4 times, respectively) was the major reason for the increase of RGR of larvae on those two suitable diets.

The growth rates for larvae transferred to either Coastal bermudagrass or common centipedegrass were comparable. These two RGR values were significantly lower than that of larvae on Tifton 10. Larvae on Coastal bermudagrass seemed to compensate for the low RCR by an increase in ECI, and larvae on common centipedegrass exhibited RCR and ECI values only slightly lower than those for larvae on Tifton 10 bermudagrass.

When larvae were transferred to Tifton 292 bermudagrass or zoysiagrass, the RGR of larvae on these two resistant grasses was lower than on any of the other grasses (Table 26). Evidently, the reduction of RCR and/or ECI for larvae on these two resistant grasses caused the lower RGR compared to larvae on other diets.

Table 26
Growth rates, consumption rates, and efficiencies of 6th-instar fall armyworm on selected grasses and pinto bean diet after initially fed on Tifton 10 bermudagrass[1]

Diets	Diet water content (%)	Growth rates		Consumption rates		Efficiency			No. of larvae
		AGR (mg/day)	RGR (mg/mg/day)	ACR (mg/day)	RCR (mg/mg/day)	AD (%)	ECD (%)	ECI (%)	(n)
Pinto bean diet	69.1d (0.2)	36.3a (1.5)	1.0a (0.01)	130.6a (6.0)	3.7a (0.1)	39.0ab (2.6)	71.4a (5.2)	28.2a (1.2)	14
Corn	83.5a (0.3)	25.4b (1.4)	0.9a (0.02)	98.8b (5.9)	3.7a (0.2)	32.8b (2.2)	79.4a (5.8)	26.3a (1.5)	14
Tifton 10 (CK) bermudagrass	72.1c (0.2)	24.5b (0.7)	0.7b (0.01)	130.9a (4.5)	4.0a (0.1)	33.6b (1.9)	59.2ab (4.2)	18.9b (0.5)	15
Coastal bermudagrass	69.5d (0.4)	16.4c (1.0)	0.6c (9.03)	68.4c (4.1)	2.4a (0.1)	33.2b (2.1)	74.8a (4.6)	24.1a (0.6)	15
Common centipedegrass	76.2b (0.4)	11.8d (0.8)	0.5c (0.03)	76.9cd (3.8)	3.6a (0.2)	38.4ab (1.6)	41.0b (2.9)	15.3b (0.6)	15
Tifton 292 bermudagrass	65.8e (0.3)	8.0d (1.2)	0.3d (0.04)	44.8e (5.0)	2.0b (0.2)	38.0ab (1.6)	48.6b (7.3)	17.6b (2.1)	12
Zoysiagrass	61.8f (0.6)	7.6d (0.8)	0.3d (0.03)	55.0de (5.7)	2.4b (0.2)	45.6a (5.1)	41.5b (8.8)	14.3b (1.5)	13
HSD[2]	1.6*	4.7*	0.1*	21.4*	0.7*	11.2*	22.0*	5.1*	

[1]All data were calculated on a dry weight basis and presented as Mean ± (1 SE).
[2]HSD. Honestly significant difference between means ($p=0.05$) (*), using Tukey's studentized range test for unequal sample sizes.

Unlike Spodoptera eridania larvae (Scriber 1979), FAW larvae were not able to compensate for high metabolic costs by increasing their consumption rates on the unsuitable host grasses (Tables 24, 25, and 26). This result suggests the hypothesis that variation in qualitative plant allelochemicals are important for plants attacked by "unadapted" herbivores (Feeny 1975, Blau et al. 1978), although further research is required to identify the allelochemical(s) in these resistant grasses and their influence on the growth performance of FAW larvae.

Several reports have illustrated that when insects are switched from one diet to another, growth rates and efficiencies of food utilization are significantly affected (Scriber 1981, Grabstein and Scriber 1982). In these sequential diet tests, the polyphagous FAW larvae also exhibited a high degree of variation in RCR, AD, and ECD as a result of feeding on various diets after they initially fed on corn or Tifton 10 bermudagrass (Tables 25, 26). However, the growth of larvae on resistant grasses was found to be improved as a result of increased RCR and/or ECD when compared with the performance value of larvae in the pinto bean diet-grass sequential treatments (Table 24). This stimulated me to examine the influence of initial diet on larval performance after they were switched to various foods.

Pinto bean diet can be effectively utilized by FAW larvae (Table 23), but utilization was even more effective after larvae had previously fed on either corn or Tifton 10

bermudagrass (Table 27). Pinto bean diet apparently contained no feeding deterrent or physical barrier (e.g., tough leaf fiber), thus, rate of food consumption was significantly increased ca. 1.3 to 1.4 times after larvae were transferred from either grasses.

By calculating the RGR values from the regression growth equation, it was found that growth rate values for most FAW larvae which previously fed on other grasses were greater than for larvae continuously fed on corn (Table 21). The same was also illustrated here for the RGR of 6th-instar FAW on various grasses (i.e., common centipedegrass, Tifton 10, and Coastal bermudagrass) prior to transfer to corn (Table 27). For the final instars which previously fed on the preferred grasses Tifton 10 or Coastal, the increase in RGR after they were transferred to corn was primarily due to an increase in ECI, but not RCR. Conversely, the significantly lower RGR for larvae on corn transferred from pinto bean diet than for larvae transferred from the other grasses was due mainly to a higher metabolic cost (indicated by the low ECD). For the larvae which initially fed on resistant common centipedegrass, both the increase in RCR and ECI caused the calculation of the extremely high RGR of larvae after they were transferred to corn (1.21 mg/mg/day). The increased consumption rates may have resulted because larvae were released from some unknown antifeedant chemical(s) in the leaves of common centipedegrass as described in Chapter IV, and also because of the increased water content in corn leaves.

Schoonhoven and Meerman (1978) interpreted that "physiological adaptation" might result in larval adaptation to the food on which they had previously fed. Grabstein and Scriber (1982) suggested that behavioral induction on a previous food can suppress the consumption of a new food. Neither of these two hypotheses can explain the result found here that larvae initially feeding on susceptible Tifton 10 or Coastal, as well as larvae initially feeding on resistant centipedegrass, achieved higher growth rates on corn compared to larvae continuously fed on corn. Different degrees mixed function oxidase(MFO) activities induced by the host grasses are suggested to interpret this situation. The increase of RCR and/or ECI in various sequential grass tests (Table 27) seemed to indicate that MFO system of FAW can be more easily induced on a grass diet if they had previously fed on some other grass, such as Tifton 10 bermudagrass. Under field conditions, the movement of FAW larvae from other pasture or turf grasses to corn seems to frequently happen whenever the grasses are not available. Thus, predictably, the growth rate of FAW larvae will increase as indicated by the increase in ECI, and the corn could be damaged more by increased consumption rate of larvae which moved from resistant grasses.

The growth of larvae on Tifton 10 bermudagrass was not statistically different for larvae fed previously on corn or Tifton 10 (Table 27). However, the mechanisms for this comparable growth rate in these two treatments were

different i.e., a higher ECI (21.50%) of larvae initially fed on corn, and a significantly higher RCR (3.96 mg/mg/day) for larvae continuously fed on Tifton 10. The larvae initially feeding on pinto bean diet, again, adapted poorly when switched to the grasses and showed significantly low RGR value. The suppression of growth rate was correlated to both the low RCR and ECI.

When larvae were transferred to the moderately preferred Coastal bermudagrass (Cahpter III), initial larval diet seemed to dramatically influence larval performance (Table 27). A depression of growth occurred for larvae continuously feeding on Coastal bermudagrass. The high metabolic cost (indicated as low ECD, 47.76%), rather than a reduced RCR, was the cause of such a low growth rate. On the other hand, the slow growth of larvae transferred from pinto bean diet was due to both a low RCR and a low ECI. For the larvae previously fed on resistant common centipedegrass, the extremely high RCR (3.19 mg/mg/day) indicated that growth was enhanced after they were transferred to Coastal bermudagrass. The high RCR was also responsible for the high RGR of larvae in centipedegrass-corn treatment.

The significantly low RCR (1.28 mg/mg/day) and ECI (5.71%) were responsible for the suppression of larval growth when 6th-instars were fed on pinto bean diet prior to transfer to the resistant centipedegrass (Table 27). The statistically same growth rates were achieved by larvae

Table 27
Influence of previous host on the growth rates, consumption rates and efficiencies of 6th-instar fall armyworm after transfer to selected grasses[1]

Indices	Larval initially fed on	Performance of 6th-instar fall armyworm after transfer to						
		Pinto bean diet	Corn	Tifton 10 bermuda-grass	Coastal bermuda-grass	Common centipede-grass	Tifton 292 bermuda-grass	Zoysia-grass
RGR (mg/mg/day)	Pinto bean diet	0.88b	0.55d	0.39b	0.29c	0.08b	0.02c	0.10b
	Corn	0.98a	0.63c	0.67a	0.51ab	0.52a	0.22b	0.14b
	Tifton 10 bermuda-grass	1.02a	0.94b	0.74a	0.57a	0.54a	0.34a	0.33a
	Coastal bermuda-grass	-	0.94b	-	0.37bc	0.61a	-	-
	Common centipede-grass	-	1.21a	-	0.66a	-	-	-
	HSD[2]	0.07*	0.10*	0.11*	0.17*	0.09*	0.07*	0.05*

Table 27--continued

Indices	Larval initially fed on	Performance of 6th-instar fall armyworm after transfer to						
		Pinto bean diet	Corn	Tifton 10 bermuda-grass	Coastal bermuda-grass	Common centipede-grass	Tifton 292 bermuda-grass	Zoysia-grass
RCR (mg/mg/day)	Pinto bean diet	2.81b	3.46b	2.28c	1.84c	1.28b	0.69c	1.10b
	Corn	3.94a	3.76b	3.08b	2.53b	3.10a	1.52b	1.38b
	Tifton 10 bermuda-grass	3.69a	3.69b	3.96a	2.40bc	3.59a	1.99a	2.39a
	Coastal bermuda-grass	-	4.30b	-	2.41bc	3.49a	-	-
	Common centipede-grass	-	5.67a	-	3.19a	-	-	-
	HSD[2]	0.37*	1.03*	0.28*	0.59*	0.62*	0.23*	0.29*

Table 27--continued

Indices	Larval initially fed on	Performance of 6th-instar fall armyworm after transfer to						
		Pinto bean diet	Corn	Tifton 10 bermuda-grass	Coastal bermuda-grass	Common centipede-grass	Tifton 292 bermuda-grass	Zoysia-grass
AD (%)	Pinto bean diet	33.40c	41.27a	37.12ab	27.44b	41.06b	28.87b	27.61b
	Corn	49.13a	34.30a	40.60a	41.33a	30.86c	28.81c	25.09b
	Tifton 10 bermuda-grass	38.99b	32.79a	33.62b	33.17ab	38.43bc	37.98a	45.62a
	Coastal bermuda-grass	-	34.68a	-	36.98ab	54.15a	-	-
	Common centipede-grass	-	35.92a	-	33.59ab	-	-	-
	HSD[2]	4.96*	12.88	3.60*	12.42*	8.20*	8.26*	10.30*

Table 27--continued

Indices	Larval initially fed on	Performance of 6th-instar fall armyworm after transfer to						
		Pinto bean diet	Corn	Tifton 10 bermuda-grass	Coastal bermuda-grass	Common centipede-grass	Tifton 292 bermuda-grass	Zoysia-grass
ECD (%)	Pinto bean diet	85.52a	49.22b	45.40b	48.13ab	16.12c	2.89b	39.49a
	Corn	53.03c	56.97ab	52.76ab	50.30ab	57.32a	47.89a	29.26a
	Tifton 10 bermuda-grass	71.35b	79.38a	59.23a	74.76a	41.03ab	48.64a	41.51a
	Coastal bermuda-grass	-	68.30ab	-	47.76b	35.66b	-	-
	Common centipede-grass	-	65.05ab	-	66.63ab	-	-	-
	HSD[2]	8.85*	28.09*	9.76*	26.80*	19.52*	12.02*	17.77

Table 27--continued

Indices	Larval initially fed on	Performance of 6th-instar fall armyworm after transfer to						
		Pinto bean diet	Corn	Tifton 10 bermuda-grass	Coastal bermuda-grass	Common centipede-grass	Tifton 292 bermuda-grass	Zoysia-grass
ECI (%)	Pinto bean diet	31.32a	17.20b	16.78b	12.51c	5.71b	4.29b	8.45b
	Corn	25.36c	17.55b	21.50a	20.29ab	17.03a	14.02a	10.97ab
	Tifton 10 bermuda-grass	28.18b	26.29a	18.87ab	24.08a	15.27a	17.59a	14.32a
	Coastal bermuda-grass	-	22.45ab	-	15.30bc	18.06a	-	-
	Common centipede-grass	-	21.36ab	-	20.81ab	-	-	-
	HSD[2]	2.13*	5.47*	3.42*	5.81*	4.57*	5.70*	3.80*

[1]All data were calculated on a dry-weight basis.
[2]HSD. Honestly significant difference (p=0.05) (*), using Tukey's studentized range test for unequal sample sizes.

initially reared on corn, Tifton 10 and Coastal bermudagrass. The mixed function oxidase (MFO) of FAW has been demonstrated to be induced to various degrees by different host plants (Yu 1982a, 1983a). For all tested microsomal oxidase activities of 6th-instar FAW after feeding on various food plants, those of larvae on corn were rated the highest, and ranged from 2 to 4 times higher than those of larvae feeding on artificial diet (Yu 1982a,b, 1983a). This may explain the lower metabolic cost (i.e., the high ECD, 57.32%) of larvae in the corn-centipedegrass transfer compared to larvae in other diets-centipedegrass treatments.

In order to examine the performance of FAW larvae switched between Coastal bermudagrass, the most popular pasture grass, and common centipedegrass, a widely grown turf grass, both the penultimate and final instars of FAW larvae were studied and the results presented in Table 28. Only the growth rates of penultimate instars were significantly different between the centipedegrass-Coastal (0.80 mg/mg/day) and Coastal-centipedegrass (0.35 mg/mg/day) treatments. The compensation for low ECD by increasing AD allowed final instar larvae to achieve high ECI (ca. 2 times that of penultimate instar larvae) on resistant centipedegrass after they were transferred from Coastal bermudagrass. Age effects on the growth performance of FAW larvae were, thus, evident. Yu (1983b) illustrated that older FAW larvae had lower insecticide susceptibility and higher detoxification capacity. Therefore, the higher growth rate

Table 28
Growth rates, consumption rates, and efficiencies of the final two fall armyworm instars when reciprocally transferred between common centipedegrass and Coastal bermudagrass[1]

Larvae initially fed on	Larvae transferred to	Leaf water content (%)	Relative growth rate (mg/mg/day)	Relative consumption rate (mg/mg/day)	Efficiency AD (%)	Efficiency ECD (%)	Efficiency ECI (%)	No. of larvae (n)
			5th-instar					
Common centipedegrass	Coastal bermudagrass	67.6b (0.004)	0.80a (0.05)	3.43a (0.20)	33.07a (3.68)	71.82a (6.48)	23.30a (1.03)	15
Coastal bermudagrass	Common centipedegrass	76.5a (0.003)	0.35b (0.07)	3.57a (0.28)	33.73a (2.60)	28.75b (3.75)	9.75b (1.49)	9
HSD[2]		0.01*	0.17*	0.71	10.77	18.48*	3.65*	

Table 28--continued

Larvae initially fed on	Larvae transferred to	Leaf water content (%)	Relative growth rate (mg/mg/day)	Relative consumption rate (mg/mg/day)	Efficiency AD (%)	Efficiency ECD (%)	Efficiency ECI (%)	No. of larvae (n)
			6th-instar					
Common centipedegrass	Coastal bermudagrass	69.6b (0.005)	0.66a (0.06)	3.19a (0.27)	33.59b (4.70)	66.63a (6.97)	20.81a (0.87)	10
Coastal bermudagrass	Common centipedegrass	76.0a (0.003)	0.61a (0.02)	3.49a (0.23)	54.15a (3.18)	35.66b (5.21)	18.06a (1.06)	9
HSD[2]		0.01	0.03	0.75	12.22*	18.64*	2.87	

[1]All data were calculated on a dry-weight basis and presented as Mean ± (1 SE).

[2]HSD. Honestly significant difference ($p=0.05$) (*), using Tukey's studentized range test for unequal sample sizes.

of older FAW on resistant centipedegrass compared to younger larvae is also correlated with the induction of higher MFO activity in older larvae.

CHAPTER VIII
CONCLUSIONS

The results obtained in this research aid in the understanding of FAW-host interactions. The preference tests indicated that the order of preference by FAW larvae for the six grasses was as follows: Tifton 10 (highly preferred) > Coastal bermudagrass > common centipedegrass > C-181 centipedegrass > Tifton 292 bermudagrass > zoysiagrass. Nitrogen fertilization may significantly influence FAW feeding behavior, biology, and also the expression of plant resistance for both common centipedegrass and Coastal bermudagrass. The Coastal bermudagrass is normally susceptible to FAW, but becomes nonpreferred with low N-fertilization.

Both preference and antibiosis tests revealed the resistance found in common centipedegrass is due to both a high level of nonpreference and intermediate level of antibiosis. The adverse biological effects, i.e., low larval weight, a delay of larval development, small pupae, and high mortality, on FAW feeding on Tifton 292 and zoysiagrass indicated the high level of nonpreference and/or antibiosis conditioning the resistance of these two grasses. Serious abnormal pupae and wing-deformity of the adult resulted when the resistant grasses were incorporated into

the artificial diet and fed to FAW larvae. Thus various types of antibiosis effects were manifested in these resistant grasses.

The sequential tests under laboratory conditions indicated that when larvae were initially fed a susceptible host such as corn, subsequent development depended on the suitability of the host on which larvae completed development. Therefore, a high degree of FAW preference for a host is not the only factor that enhanced development, but the ability of the insect to adapt to the new host after migration or dispersal is also important.

The length of time that FAW larvae fed on a suitable host also influenced subsequent development. As an illustration, the longer that FAW larvae fed on corn prior to transfer to either a susceptible or a resistant host, the faster they completed larval development and the less mortality occurred. The expression of resistance of a host plant on an insect, thus, can be altered by both the initial host and the time that the insect fed on the initial host.

The time that FAW larvae fed on the resistant host was highly important. The FAW larvae that fed on the resistant host for only a short time were better able to compensate for and/or recover from the antibiosis effects than were larvae that had fed for an intermediate time (i.e., 6 days) on the resistant host. However, this trend was reversed when the larvae fed on the resistant host for a longer period of time, in that the "superior" individuals

that had been selected completed development rapidly, suffered low mortality, and produced heavier pupae once they were transferred to a susceptible host.

Tests of quantitative food utilization by FAW larvae showed that the amount of food consumed by larvae varied among instars on the same diet and among different diets. The most destructive stages of FAW were the last two instars, during which more than 75% of total amount of food is consumed.

The suitability of pinto bean diet to FAW was reflected by the low metabolic costs (i.e., high efficiency of conversion of digested food, ECD) of processing it when compared with other susceptible grasses such as corn or Tifton 10 bermudagrass. Both high consumption rate (RCR) and high efficiency of conversion of ingested food into biomass (ECI) contribute to the high growth rate of FAW larvae feeding on corn after they were transferred from other resistant or susceptible grasses. When FAW larvae were switched from susceptible to resistant grasses, the reductions of RCR and/or ECD indicated that the significant low growth rate of larvae occurred.

It appears that the highly polyphagous nature of FAW larvae may have developed as a mechanism that enhances survival. The FAW egg masses may be laid on a host with a high level of antibiosis or nonpreference larval resistance, but the larvae readily disperse and adapt to new hosts that may enhance survival and development. Therefore, the selection

of resistant hosts or agroecosystem diversification to manage FAW populations should be carefully considered since FAW larvae are highly mobile and polyphagous.

Although many interesting interactions of FAW and tested grasses in these series of studies have been found, additional studies are warranted such as (1) the study concerning the interactions of insect behavior and plant resistance (e.g., ovipositional preference), (2) the influence of other environmental factors (e.g., temperature, relative humidity, phenology of plants) on the expression of plant resistance, (3) isolation, identification, and bioassay of antifeeding chemical(s) from the resistant plant, (4) the genetic factors affecting expression and stability of resistance, and (5) the breeding approaches in grasses, etc., before this pest can be successfully managed.

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BIOGRAPHICAL SKETCH

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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